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STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 9. THE STERLITAMAKIAN BRACHIOPOD FAUNA OF THE CUNCUDGERIE SANDSTONE, CANNING BASIN

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ARCHBOLD, N. W., 1990:05:31. Studies on Western Australian Permian brachiopods 9. The Sterlitamakian brachiopod fauna of the Cuncudgerie Sandstone, Canning Basin. *Proceedings of the Royal Society of Victoria* 102(1): 1-13. ISSN 0035-9211.

The brachiopod fauna from isolated outcrops of the Early Permian Cuncudgerie Sandstone in the southern Canning Basin is reviewed and described. New species described are *Tornquistia subquadratus* and *Cyrtella kooi*. The fauna is a correlative of other brachiopod faunas of Early Permian (Sterlitamakian) stratigraphical units elsewhere in Western Australia (Perth, Carnarvon and northern Canning Basins).

THE ONSHORE Canning Basin of Western Australia measures some 800 km from north to south, 950 km from east to west and covers an area of 430,000 km² (Towner & Gibson 1983). Structural subdivisions of the basin are reviewed by Playford et al. (1975) and Towner & Gibson (1983). To date, most described Permian brachiopod faunas of the basin are from the thick sequences of the Fitzroy Trough in the north (e.g. see stratigraphy and faunal lists provided by Guppy et al. 1958). Thin Permian sequences with isolated outcrops occur in the south of the basin, in the region of the Anketell Shelf (Playford et al. 1975: 364, fig. 54). Limited brachiopod faunas from these outcrops have been recorded in numerous reports (Dickins & Thomas 1956, Dickins 1961, Dickins 1976; the last of these was published in 1983 as part of a microfiche appendix in Towner & Gibson 1983 who consolidated all previous reports). A few brachiopod specimens have been figured by Thomas (1971), Archbold (1983, 1986) and Archbold & Thomas (1984a).

Of the southern Canning Basin faunas, that of the Cuncudgerie Sandstone (Traves et al. 1956) is the most diverse and is the subject of the present study. The Cuncudgerie Sandstone has been correlated by previous workers with the Nura Nura Member of the Poole Sandstone and with the marine horizon at the base of the Poole Sandstone in the St George Range area (both northern Canning Basin). This correlation is supported by the present study although there is by no means a complete identity of faunas. This may be due to inadequate sampling of the units involved or differences in biofacies. Towner & Gibson (microfiche appendix number 5 in Towner & Gibson

1983) considered the "Cuncudgerie facies" to be a more clastic facies equivalent of the Nura Nura member.

AGE, PRESERVATION AND COLLECTIONS

The described assemblage exhibits significant links with the fauna of the Sterlitamakian (Late Sakmarian) Callytharra Formation of the Carnarvon Basin. The age of that formation is well constrained by ammonoids as indicated by Archbold (1982a).

Preservation of the material is of variable quality. Internal and external moulds, usually ferruginous, preserve sharp details of internal muscle scars and external ornament. Natural ferruginous casts of shells preserve less fine details but provide details of the gross form of the specimens. Many specimens are incomplete.

All specimens are registered with the Commonwealth Palaeontological Collections (CPC) of the Bureau of Mineral Resources, Geology and Geophysics, Canberra. Specimens were collected by W. J. Koop (West Australian Petroleum Pty Ltd) in 1963 (locality number TK5A) and by field parties of the Bureau of Mineral Resources.

SYSTEMATIC PALAEOLOGY

Order STROPHOMENIDA Öpik, 1934
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETACEA Waagen, 1884
Family ORTHOTETIDAE Waagen, 1884
Subfamily ORTHOTETINAE Waagen, 1884

Genus *Permorthotetes* Thomas, 1958

Type species. Permorthotetes callytharrensensis Thomas, 1958.

Comments. *Permorthotetes* was regarded by Manankov (1979) as a synonym of *Orthotetes* Fischer de Waldheim, 1829, but I agree with Manankov's (1973) earlier view that these genera are distinct.

Permorthotetes lindneri Thomas, 1958

Fig. 1A-C

Permorthotetes lindneri Thomas 1958: 92, pl. 1, figs 1-4, pl. 2, figs 1-3, pl. 3, figs 1-6.—Guppy et al. 1958: 54.—Thomas in Dickins 1976: 99.

Orthotetid.—Dickins 1976: 100.

Material. CPC 28024-28025, portion of a ventral valve external mould and portion of a dorsal valve external mould from locality TK5A, Scott Bluff, southern Canning Basin (collected by W.J. Koop).

Comments. The nature of the flat ventral valve, fine costellae and step-like lamellae permit assignment of the material to *P. lindneri* as identified by Thomas (in Dickins 1976). Thomas (1958: 92-96) fully described *P. lindneri* and compared it with other Western Australian representatives of *Permorthotetes*.

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETACEA Bronn, 1862

Family ANOPLIIDAE Muir-Wood, 1962

Discussion. Since the reviews by Archbold (1980, 1981), this family has been investigated by Afanas'yeva (1984a, b). She stressed the appearance of heterochronous homeomorphs and considered it preferable to subdivide the family on the basis of dorsal internal features rather than on external ornament. The subfamily Tornquistiinae, possessing low radial lines of fused papillae in the dorsal interior, was separated by Afanas'yeva (1984a) from the

Anopliinae, possessing paired radial ridges in the dorsal interior. Dorsal features do not appear to be a reliable criterion for subfamilial classification, however, as it is difficult to place in separate subfamilies the type species of *Anoplia* and *Tornquistia*, the dorsal interiors of which possess similar paired interior radial ridges (see Muir-Wood 1962, pl. 5, figs 16, 21).

Subfamily ANOPLIIDAE Muir-Wood, 1962

Genus *Tornquistia* Pacckelmann, 1930

Type species. Leptaena (Chonetes) polita McCoy, 1852.

Diagnosis. Anopliinids with short lateral septa and prominent accessory septa in dorsal interior. Ventral interior with short, thin median septum. Shell exterior smooth.

Discussion. *Tornquistia* was reviewed by Archbold (1980, 1981) who substantially restricted the Permian palaeogeographical range of the genus to Western Australia, Thailand, the Salt Range in Pakistan, Eastern Siberia and Arctic North America. Many Permian species of the genus possess dorsal interior paired radial ridges that are less distinct than those of the type species (e.g. see Afanas'yeva 1977, Archbold 1980).

Tornquistia subquadratus sp. nov.

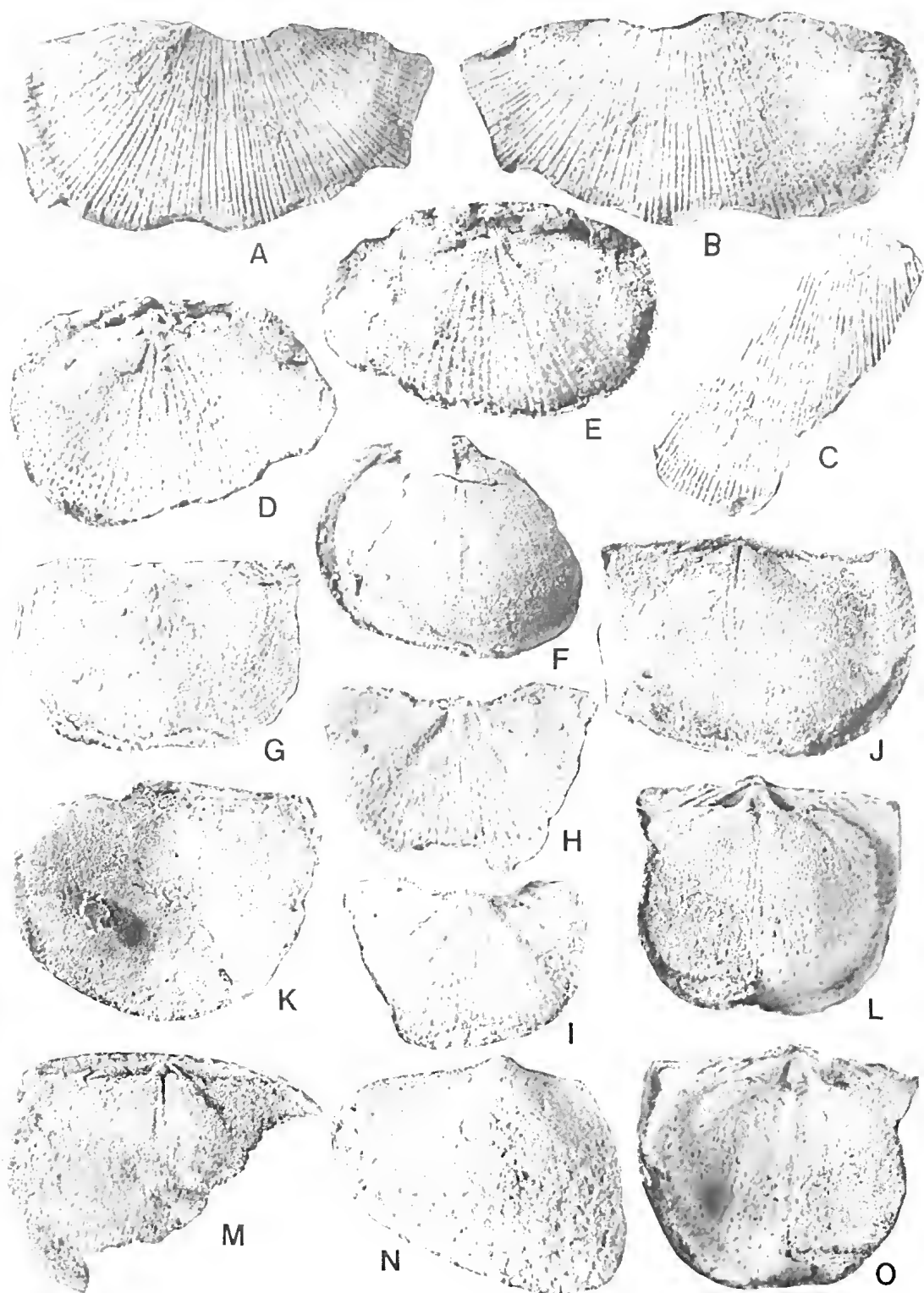
Fig. 1D-O

"*Chonetes*" sp.—Dickins 1976: 99.

Holotype. CPC 28026, an internal mould of a dorsal valve.

Other material and locality. CPC 28026-28034, 2 dorsal valve internal moulds, 2 dorsal valve external moulds, 4 ventral valve internal moulds and 1 incomplete ventral valve external mould as well as numerous fragments of moulds; all from locality TK5A, Scott Bluff, east side of Lake Blanche, southern Canning Basin; collected by W. J. Koop.

Fig. 1. A-C, *Permorthotetes lindneri* Thomas. A, B, CPC 28024, incomplete external mould of ventral valve and latex cast, $\times 1.5$. C, CPC 28025, latex cast of incomplete external mould of dorsal valve, $\times 1.5$. D-O, *Tornquistia subquadratus* sp. nov. D, E, CPC 28026, holotype, internal mould of dorsal valve and latex cast, $\times 5.0$. F, CPC 28027, ventral valve internal mould, $\times 5$. G, CPC 28029, dorsal valve internal mould and latex cast, $\times 5$. J, CPC 28030, ventral valve internal mould, $\times 5$. K, CPC 28031, latex cast of dorsal valve external mould, $\times 5$. L, O, CPC 28032, internal mould of ventral valve and latex cast of mould, $\times 5$. M, CPC 28033, internal mould of ventral valve, $\times 5$. N, CPC 28034, latex cast of ventral valve external mould, $\times 5$.



Measurements. In mm, e = estimate.

Specimen	Maximum width	Ventral height	Dorsal height	Hinge width
CPC 28026	12.6	—	7.9	—
CPC 28028	10.8	—	6.9	9.4
CPC 28029	12.8	—	8.8	11.2e
CPC 28030	11.0e	8.5	—	—
CPC 28031	14.0e	9.4	—	12.0e
CPC 28032	11.6e	8.8	—	11.6e
CPC 28033	11.5e	—	—	11.0e

Diagnosis. Medium sized *Tornquistia* with subquadrate shells at maturity. Maximum width often greater than hinge width at maturity. Dorsal septa weakly developed including centrally developed median septum.

Description. Ventral valve of pronounced convexity with distinctly inflated mesial portion of valve. Dorsal valve concave with demarcated deeper central region. Greatest width of shell anterior of hinge line at about one-third to one-half shell length. Exterior of shell smooth with faint growth lines. Interareas low, cardinal spines apparently short. Ventral umbo low.

Ventral interior with blunt, relatively large teeth. Delthyrium distinct with pronounced thickening of shell beneath it. Minute pseudodeltidium in apex of delthyrium. Median septum sharp posteriorly, extending weakly anteriorly for about one-half of valve length. Muscle scars usually weakly impressed. Valve floor, except for smooth muscle scars, marked by weakly developed radial rows of pustules. Weakly impressed parallel vascular trunks form low ridges adjacent to median septum.

Cardinal process poorly known. Socket plates short but distinct. Lateral and accessory septa relatively weakly developed and separated by several rows of radial pustules which continue to anterior of valve. Short median septum developed in valve centre with radial row of pustules anteriorly.

Discussion. *Tornquistia subquadratus* is distinguished from other Western Australian Permian members of the genus by its more subquadrate outline with a maximum width anterior of the hinge line. *T. gregoryi* Archbold, 1981 from the Late Artinskian Wandagee Formation rarely exhibits a subquadrate outline but that species is distinguished from *T. subquadratus* by its incipient ventral fold. *T. occidentalis* Archbold, 1980 from the Sterlitama-

kian Callytharra Formation of the Carnarvon Basin is smaller and has a more trigonal shell but its internal structures appear similar to those of *T. subquadratus*.

Tornquistia gibbera Afanas'yeva, 1977 from the Late Carboniferous Paren Horizon of the Kolyma-Omolon Massif is slightly less subquadrate than *T. subquadratus* and possesses less well defined rows of dorsal internal radial papillae. The younger *T. tropicalis* Grant, 1976 from the Late Artinskian of Thailand is a triangular species unlikely to be confused with the new species, and is stated to have a short dorsal median septum. The Sakmarian *Tornquistia* sp. (Bamber & Waterhouse 1971, pl. 15, figs 16, 17) from northern Yukon Territory, Canada, is larger than *T. subquadratus* and possesses finer rows of dorsal interior radial papillae.

Suborder STROPHALOSIIDINA Waterhouse, 1975

Superfamily STROPHALOSIACEA Schuchert, 1913

Family STROPHALOSIIDAE Schuchert, 1913
Subfamily STROPHALOSIINAE Schuchert, 1913

Genus *Strophalosia* King, 1844

Type species. Strophalosia gerardi King, 1846

Discussion. The morphology, type species and palaeogeographical distribution of the genus were reviewed by Archbold (1986).

Strophalosia irwinensis Coleman, 1957

Fig. 2A-E

Strophalosia cf. *irwinensis*.—Dickins 1976: 99.

Strophalosia irwinensis.—Archbold 1986: 99-102, figs 1A-Z, 4A-I (with synonymy).

Material. Three internal moulds of ventral valves (CPC 24429-24430, CPC 28035) from locality TK5A, Scott Bluff, collected by W. J. Koop.

Comments. Two of these specimens were figured by me previously (Archbold 1986, fig. 1Y,Z) but they are refigured herein in magnified format to show the internal valve details including the muscle scars. The size and outline of the specimens and the nature of the muscle scars leave little doubt as to the assignment of the specimens to Coleman's species, despite the absence of dorsal valve details. *S. irwinensis* is well known from Sterlitamakian units in the Perth and Carnarvon Basins (Archbold 1986).

Superfamily AULOSTEGACEA Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE Muir-Wood & Cooper, 1960

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

Genus *Aulosteges* von Helmersen, 1847

Type species. Orthis wangenheimi de Verneuil, 1845
(= *Aulosteges variabilis* von Helmersen, 1847).

Aulosteges cf. *baracoodensis* Etheridge, 1903

Fig. 3A-C

cf. *Aulosteges baracoodensis* Etheridge 1903: 22, pl. 2, figs 1-2a.—Hosking 1933: 32, pl. 1, figs 1a-c, pl. 2, figs a, b.—Coleman 1957: 36, pl. 1, figs 1, 3, 4, 6.

cf. *Aulosteges lyndonensis* Coleman 1957 (partim.), pl. 4, figs 9, 10 (*non cet.*).

Aulosteges. —Dickins 1976: 100.

Material. One natural cast of a ventral valve with attached ear of dorsal valve and one external mould of the anterior of a dorsal valve (CPC 28036-28037) from BMR locality T127, Scott Bluff, Lake Blanche (22°31'06"S, 123°14'06"E), collected by BMR field parties in 1975.

Comments. The Aulosteginae is represented in the Scott Bluff collections by some nine speci-

mens, two of them belonging to *Aulosteges* itself. On the basis of shell shape, the low convexity of the ventral valve, the apparently relatively low ventral interarea and the fine to medium sized, relatively closely spaced spine bases on the ventral valve, comparison with *A. baracoodensis* is indicated. A natural cast of a ventral valve (CPC 28036) possesses a clearly demarcated small ear and recalls a specimen from the Callytharra Formation assigned to *A. lyndonensis* by Coleman (1957, pl. 4, figs 9, 10). Coleman's specimen is herein assigned to *A. baracoodensis* on the basis of its relatively closely spaced ventral spine bases. An incomplete external mould of a dorsal valve is also compared with *A. baracoodensis* on the basis of a low dorsal median fold. Other incomplete external moulds of dorsal valves from Scott Bluff show very minor development of a similar feature and are discussed under *Taeniothaerus* cf. *irwinensis*. *A. baracoodensis* is known from the Sterlitamakian Callytharra Formation (Carnarvon Basin) and the Fossil Cliff Member of the Holmwood Shale (Perth Basin).

Genus *Taeniothaerus* Whitehouse, 1928

Type species. Productus subquadratus Morris, 1845.

Comments. The type species has been redescribed by Parfrey (1983). Reports of the species

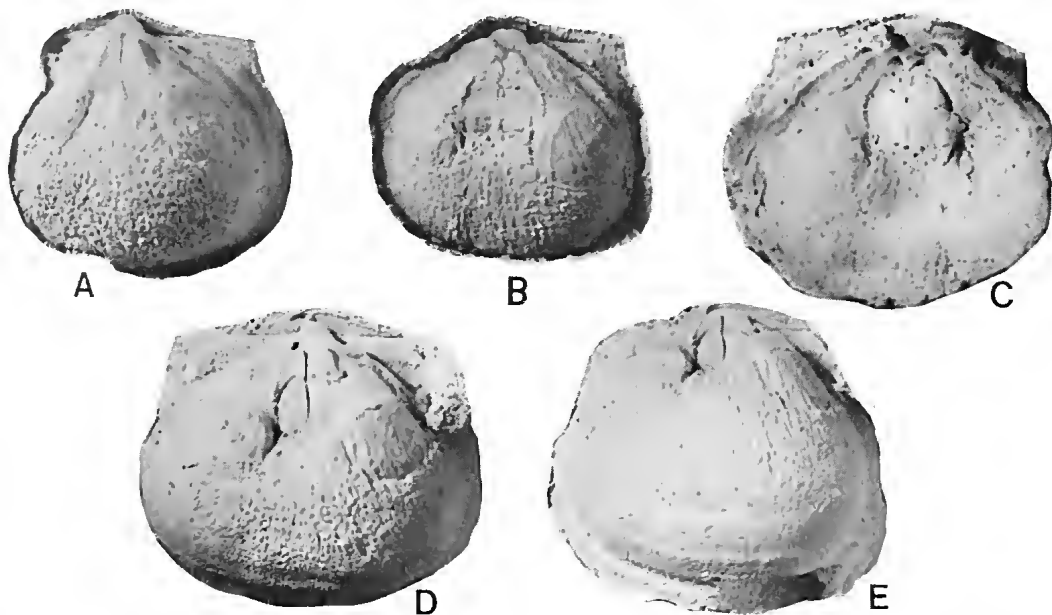
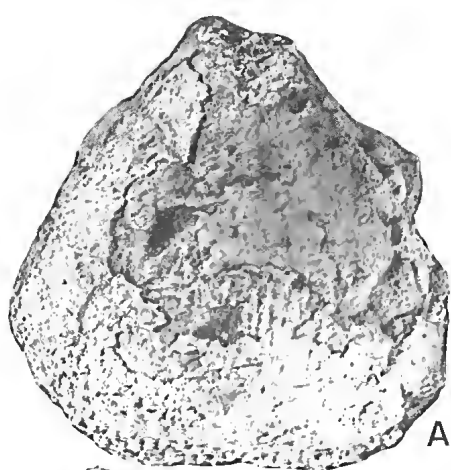


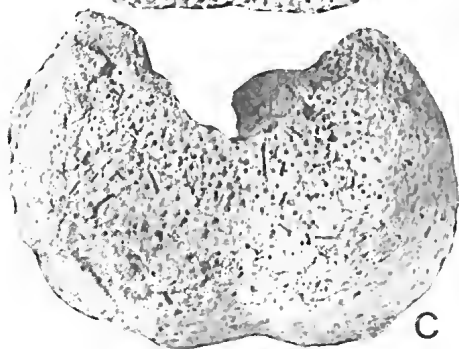
Fig. 2. A-E, *Strophalosia irwinensis* Coleman. A, CPC 28035, internal mould of ventral valve, $\times 2$. B, C, CPC 24430, internal mould of ventral valve and latex cast of mould, $\times 2.3$ and $\times 2.6$. D, E, CPC 24429, internal mould of ventral valve in ventral and anterior views, $\times 2.5$.



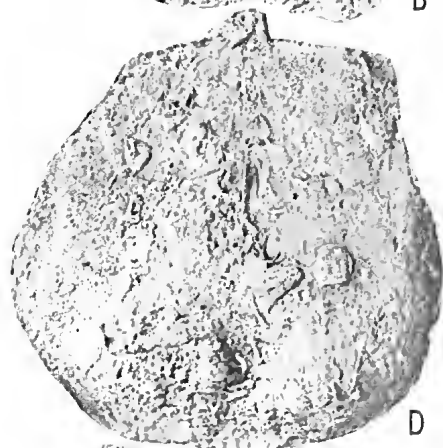
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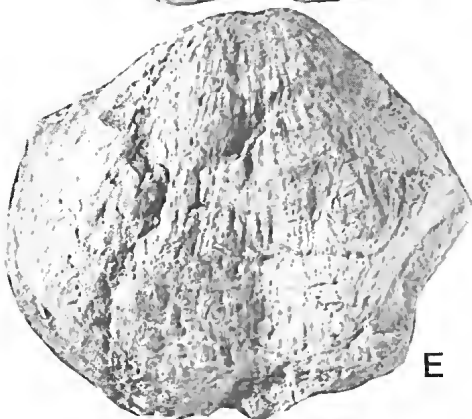
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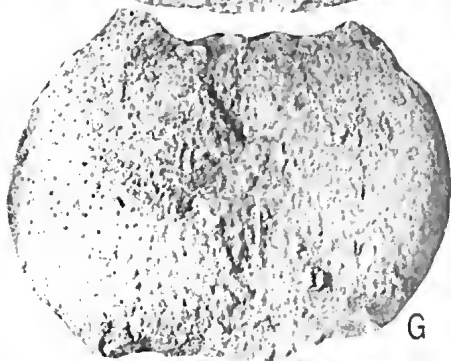
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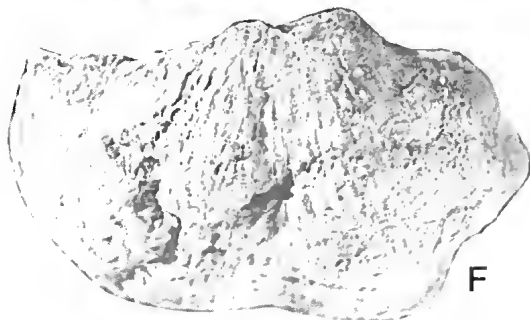
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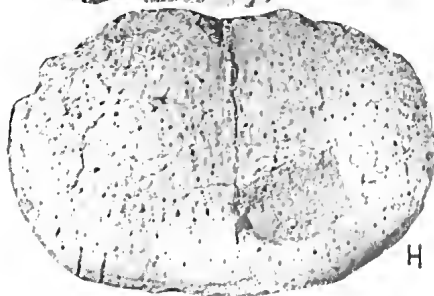
E



G



F



H

from Western Australia require critical examination.

Taeniothaerus cf. *irwinensis* Coleman, 1957

Figs 3D–H, 4A–E

cf. *Taeniothaerus irwinensis* Coleman 1957: 93, pl. 11, figs 13, 14, pl. 12, figs 1–6.

Taeniothaerus.—Dickins 1976: 99, 100.

Material. Two incomplete internal moulds of ventral valves and 4 incomplete external moulds of dorsal valves (CPC 28038–28041, 28043, 28044) from BMR locality T127, Scott Bluff, Lake Blanche, collected from BMR field parties in 1975. One external mould of the anterior of a dorsal valve (CPC 28042) from locality TK5A, collected by W. J. Koop.

Comments. The rounded shell outline, short hinge line and the external ornament of spine bases indicate a close comparison of the material with *T. irwinensis* from the Sterlitamakian Fossil Cliff Member of the Holmwood Shale (Perth Basin). Other Western Australian species assigned to *Taeniothaerus* by Coleman (1957) possess wider hinge lines and a more sub-quadrate or elongate shell outline. Some species such as *T. miniliensis* Coleman possess much finer ornament than *T. irwinensis*.

Suborder PRODUCTIDINA Waagen, 1883

Superfamily LINOPRODUCTACEA Stehli, 1954

Family LINOPRODUCTIDAE Stehli, 1954

Subfamily LINOPRODUCTINAE Stehli, 1954

Genus *Cancrinella* Fredericks, 1928

Type species. *Productus cancrini* de Verneuil, 1842.

Discussion. Archbold (1983) discussed the type species and its date of authorship.

Cancrinella irwinensis Archbold, 1983

Fig 4F–G

Linoproductus sp.—Thomas in Dickins 1961: 288.—Thomas in Dickins 1976: 98.

Cancrinella sp.—Dickins 1976: 100.

Cancrinella irwinensis Archbold 1983: 240, fig. 1C–P (with synonymy).

Material. Two natural casts of ventral valves, one sub-mature (CPC 19918) and one juvenile (CPC 28045), from BMR locality T127, Scott Bluff, collected by BMR field parties in 1975.

Comments. The specimens belong to the *C. cancriniformis* species group characterised by distinct, relatively fine rugae across the venter of the shell and distinct elongate ventral spine bases (see Archbold 1983: 240). Such species are restricted to Early Permian faunas of Western Australia where the best known species is *C. irwinensis* Archbold from the Sterlitamakian Fossil Cliff Member and Callytharra Formation. The spacing of the spine bases on the present material is particularly close to that of *C. irwinensis* and so the material is referred to that species.

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SYRINGOTHYRIDACEA Fredericks, 1926

Family SYRINGOTHYRIDIDAE Fredericks, 1926

Subfamily PERMOSYRINXINAE Waterhouse, 1986

Genus *Cyrtella* Fredericks, 1924

Type species. *Cyrtella kulikiana* Fredericks, 1916.

Discussion. *Punctocyrtella* Plodowski, 1968 is clearly closely related to *Cyrtella* and may be synonymous with it (Thomas 1971, Waterhouse 1987). Thomas (1971) and Archbold & Barkham (1989) stressed the presence of a grooved fold in *Cyrtella* (or *Punctocyrtella*) but this may be a variable feature (Waterhouse 1987) and does not appear to be present in the new species described below. The relationship of *Cyrtella* to other genera was discussed by Thomas (1971), Grigor'yeva (1977), Waterhouse (1987) and Solomina (1988).

Fig. 3. A–C, *Aulosteges* cf. *baracoodensis* Coleman. A, B, CPC 28036, natural cast of shell in ventral and dorsal views, $\times 1$. C, CPC 28037, incomplete external mould of dorsal valve, $\times 1$. D–H, *Taeniothaerus* cf. *irwinensis* Coleman. D, CPC 28038, natural cast of dorsal valve in internal view, $\times 1$. E, F, CPC 28039, internal mould of ventral valve in ventral and posterior views, $\times 1$. G, CPC 28028, external mould of dorsal valve, $\times 5$. H, I, CPC 28040, incomplete natural cast of dorsal valve, $\times 1$. H, CPC 28041, incomplete natural cast of dorsal valve, $\times 1$.

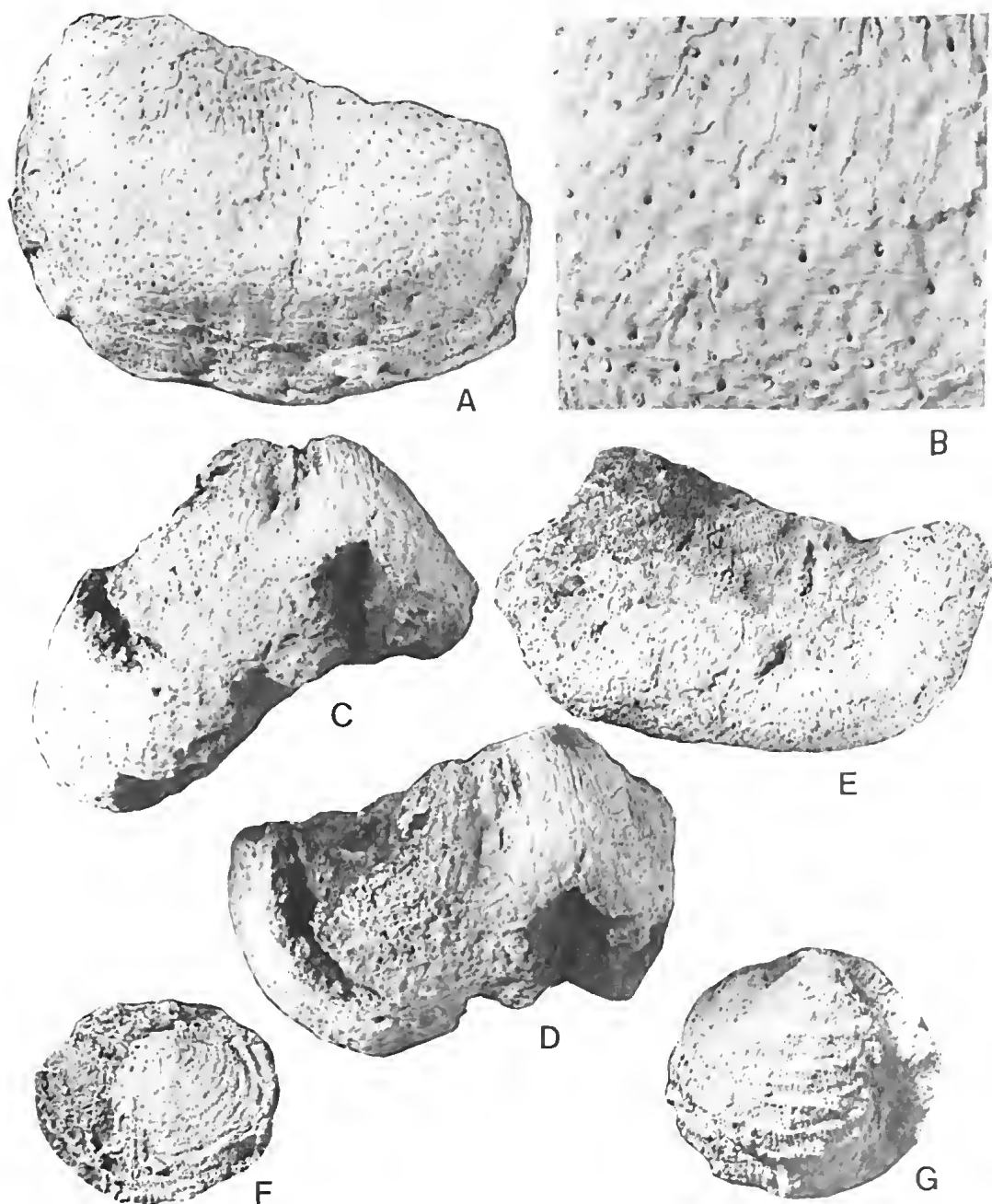


Fig. 4. A–E, *Taeniothaerus* cf. *irwinensis* Coleman. A, B, CPC 28042, incomplete external mould of dorsal valve, $\times 1$, portion enlarged, $\times 3.5$. C, D, CPC 28043, incomplete ventral valve in ventral and posterior views, $\times 1$. E, CPC 28044, incomplete external mould of dorsal valve, $\times 1$. F, G, *Cancrinella irwinensis* Archbold. F, CPC 28045, incomplete natural cast of juvenile ventral valve, $\times 2.5$. G, CPC 19918, natural cast of ventral valve, $\times 2$.

Cyrtella koopii sp. nov.

Fig. 5A-E

Pseudosyrinx sp. aff. *nagmargensis* (Bion).—Thomas in Dickins 1976: 99.

Etymology. Named after W. J. Koop, collector of the holotype.

Holotype. CPC 28046, an internal mould of a conjoined shell from locality TK5A, Scott Bluff.

Diagnosis. Large, wide species with wide, relatively deep sulcus; dorsal fastigium apparently grooved posteriorly but flat anteriorly; ventral adminicula short; 9 to 10 broadly rounded, coarse costae on each flank.

Description. Internal mould large, transverse (estimated 100 mm wide). Anterior commissure sinuous with prominent fold. Ventral valve massively thickened posteriorly (ventral interarea of unknown height). Dorsal valve not thickened greatly; external ornament clearly defined on interior. Sulcus deeply rounded, extended into prominent ventral tongue. Ventral external ornament poorly impressed on anterior of valve interior. Costae apparently coarse, low and gently rounded; number not clear.

Dental plates stout with blunt thick teeth and short thickened adminicula. Ventral muscle field prominent (20 mm wide, 25 mm long); diductor muscle scars longitudinally striate anteriorly, radially striate posteriorly; adductor muscle scar essentially smooth. Posterior part of muscle field bisected by apical callus. Interior of ventral valve either side of muscle field deeply pitted; remainder of valve interior smooth.

Dorsal interior with prominent fastigium, flattened anteriorly but possibly with groove posteriorly. Flanks of valve with up to 10 broad, flattened costae (up to 3 mm wide at anterior of valve). Cardinal process relatively small (5 mm wide); socket plates stout. Thin dorsal septum arises 3 mm anteriorly of cardinal process, extends approximately two-thirds of valve length (25 mm). Minute pustules scattered on mould surface indicate punctate shell.

Discussion. Although based on only one internal mould, the new species is named in view of the distinctive nature of the fastigium and the relatively coarse costae. *Cyrtella australis* Thomas (1971) from the Lyons Group and Callytharra Formation has finer, more numerous costae

than the new species and a distinct dorsal groove on the fastigium. *Cyrtella nagmargensis* (Bion, 1928; see also Reed, 1932) is characterised by 10 to 15 internal costae and a distinct furrow on the fastigium. Specimens of *C. nagmargensis* from the Sakmarian of Afghanistan (Termier et al. 1974) are comparable with those from Kashmir, but specimens attributed to this species from the Sakmarian of Tibet (Yang & Fan 1983, pl. 3, figs 2-5; Hu 1983, pl. 3, figs 17-23; Jin 1985, pl. 1, fig. 23) possess finer, sharper and more numerous costae than *C. koopii*.

Cyrtella kulikiana (Fredericks, 1916; see also Ifanova 1972) is a large species from the Artinskian and Kungurian of Northern European Russia and possesses more numerous costae than the new species.

Genus *Myodelthyrium* Thomas, 1986

Type species. *Pseudosyringothyris dickinsi* Thomas, 1971

Myodelthyrium dickinsi (Thomas, 1971)

cf. *Pseudosyrinx* sp. nov.—Dickins & Thomas 1956: 52.

Pseudosyrinx sp. nov.—Thomas in Dickins 1961: 288.

Pseudosyringothyris dickinsi Thomas 1971: 140, pl. 10, figs 1-5, pl. 11, figs 1, 2, pl. 12, figs 1-4, pl. 13, fig. 3, pl. 29, fig. 7.

Comments. Thomas (1971, pl. 13, fig. 3a, b) figured an external mould of a ventral interarea (CPC 1643) from the Cuneudgerie Sandstone in Well 27, in the southern central part of the Canning Basin (22°49'S, 123°40'E). No new material of this species is available from the Cuneudgerie Sandstone.

Superfamily SPIRIFERACEA King, 1846

Family SPIRIFERIDAE King, 1846

Subfamily TRIGONOTRETINAE Schuchert, 1893

Genus *Trigonotreta* Koenig, 1825

Type species. *Trigonotreta stokesii* Koenig, 1825

Discussion. The relationship of *Trigonotreta* to *Neospirifer* and the reasons for assigning various Western Australian spiriferid species to *Trigonotreta* have been discussed by Archbold & Thomas (1984b, 1986).

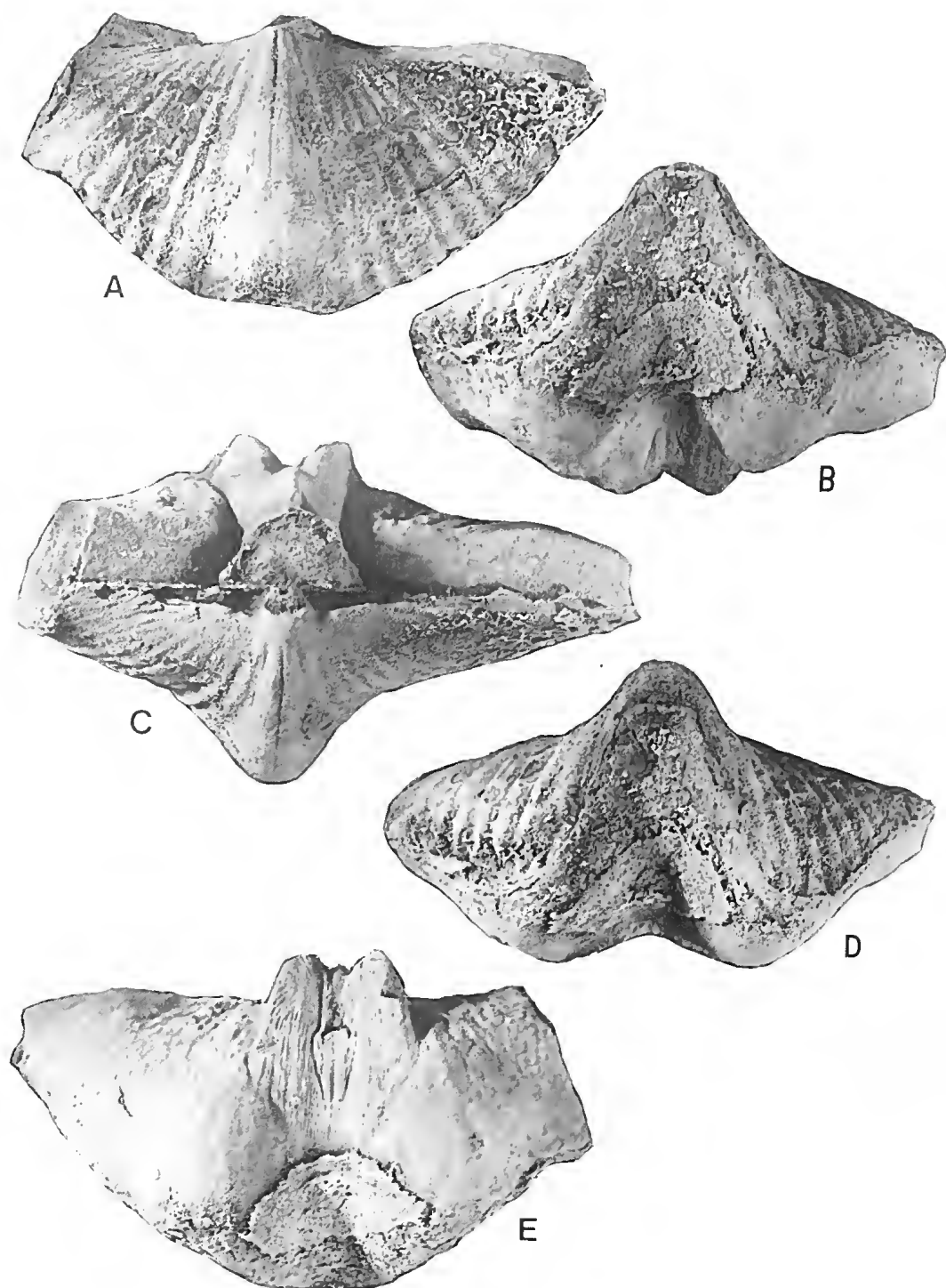


Fig. 5. A-E, *Cyrtella koopii* sp. nov., CPC 28046, holotype, internal mould in dorsal, antero-ventral, posterior, anterior and ventral views, $\times 1$.

Trigonotreta neoaustralis Archbold & Thomas, 1986

Fig. 6A-I

Neospiriferid.—Dickins 1976: 100.

Trigonotreta neoaustralis Archbold & Thomas 1986: 152, figs 16A-J, 17A-L (with synonymy).

Material. CPC 28047-28049, a natural cast of an immature conjoined shell and two incomplete casts of juvenile dorsal valves from locality T127; and CPC 28050, a ventral valve internal mould from locality TK5A.

Comments. The distinctive transverse shell out-

lines, nature and bundling of the costae and prominent growth lamellae permit ready assignment of the specimens to *Trigonotreta neoaustralis*, a species from the Sterlitamakian Fossil Cliff Member and the Callytharra Formation, and the Aktastinian Jimba Jimba Calcarenite. The specimens from locality T127 are juvenile and immature representatives of the species and hence exhibit the transverse shell outline characteristic of these ontogenetic stages (Archbold & Thomas 1986). The ventral valve internal mould represents a sub-mature specimen and possesses the characteristic bulbous apical callosity of the genus.

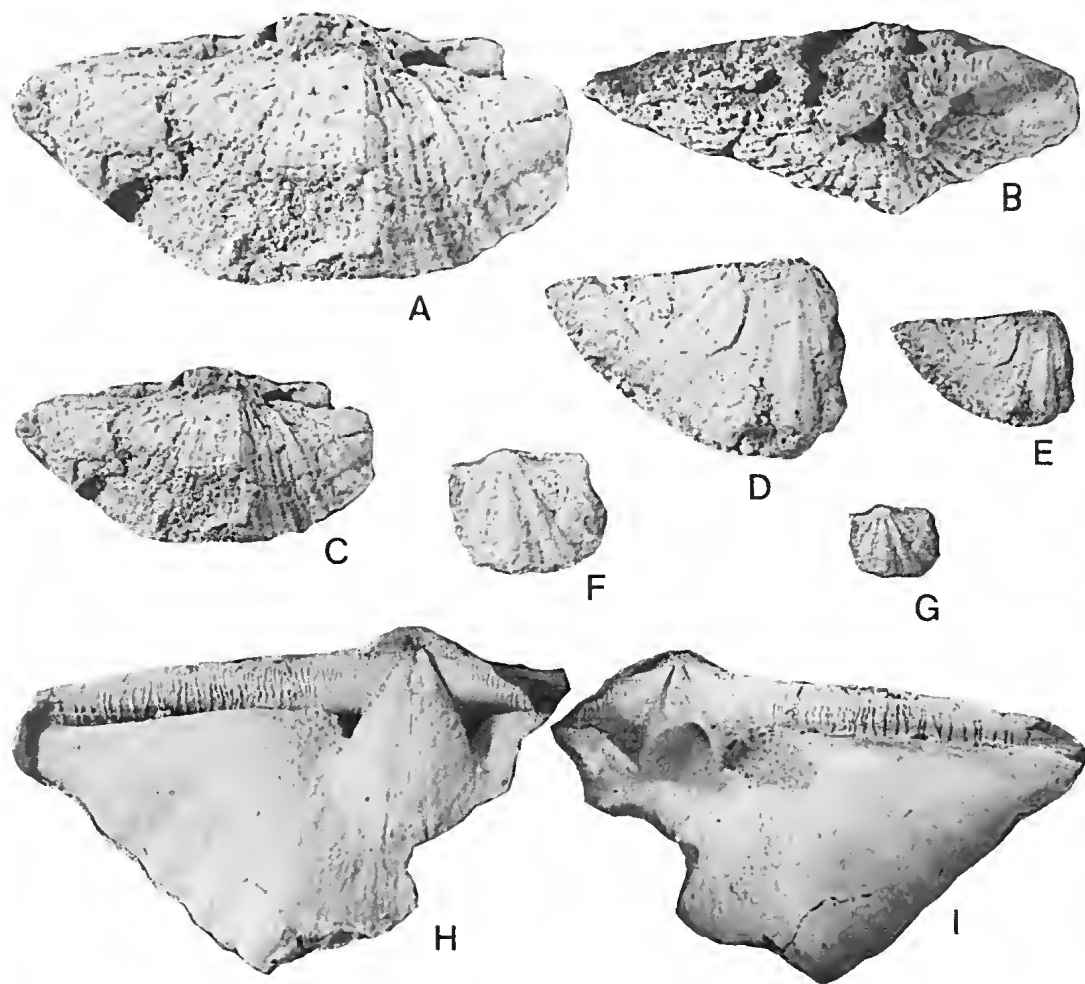


Fig. 6. A-I, *Trigonotreta neoaustralis* Archbold & Thomas. A-C, CPC 28047, natural cast of shell in dorsal, posterior and dorsal views, $\times 1.8$, $\times 1.6$, $\times 1$. D, E, CPC 28048, natural cast of dorsal valve, $\times 2$ and $\times 1$. F, G, CPC 28049, natural cast of dorsal valve, $\times 2$ and $\times 1$. H, I, CPC 28050, internal mould of ventral valve and latex cast of mould, $\times 1.8$.

Superfamily RETICULARIACEA Waagen, 1883
 Family ELYTHIDAE Fredericks, 1924
 Subfamily ELYTHINAE Fredericks, 1924

Genus *Spirelytha* Fredericks, 1924

Type species. *Spirelytha pavlovae* Archbold & Thomas, 1984.

Spirelytha cf. *fredericksi* Archbold & Thomas, 1984.

Phricodothyris sp. nov.—Dickins 1976: 99.

Spirelytha sp. cf. *S. fredericksi* Archbold & Thomas 1984: 322, fig. 4S–W.

Comments. The review of Western Australian representatives of the Elythidae by Archbold & Thomas (1984a) re-established *Spirelytha* in modern terms. Two specimens from Scott Bluff were figured in that study (CPC 24225, an internal mould of a complete shell collected by W. J. Koop, and CPC 24227, an incomplete natural cast of a ventral valve collected by the 1975 BMR field parties). The specimens were noted by Archbold & Thomas (1984a: 323) to be closest in morphological details to their *S. fredericksi* but to differ from that species in possessing a more strongly developed sulcus and fold, and in the presence of minute dorsal adminicula (the latter considered to be of infraspecific importance).

Since the Western Australian study, Klets (1987) has investigated *Spirelytha* from the Southern Verkhoyan, USSR and has identified *S. fredericksi* among his species. The Early Permian Verkhoyan species from the Sigskaya Suite is comparable to true *S. fredericksi* and lacks the more strongly developed sulcus and fold of the present material.

ACKNOWLEDGEMENTS

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TAXONOMY OF THE LARVAE, PUPAE AND FEMALES OF THE VICTORIAN SPECIES OF *CHIMARRA* STEPHENS (TRICHOPTERA: PHILOPOTAMIDAE) WITH NOTES ON BIOLOGY AND DISTRIBUTION

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CARTWRIGHT, D. I., 1990:05:31. Taxonomy of the larvae, pupae and females of the Victorian species of *Chimarra* Stephens (Trichoptera: Philopotamidae) with notes on biology and distribution. *Proceedings of the Royal Society of Victoria* 102(1): 15–22. ISSN 0035-9211.

The two species of *Chimarra* Stephens known from Victoria conform in most features with congeners described from overseas. Keys are provided for identification of adult males and females, pupae and larvae of the Victorian species, and information on the distribution of both species in Victoria as well as distribution records for the Yarra River system are presented. Details of the life history of *Chimarra australica* are included, as well as information on mesh size of the capture nets for both species.

THE GENUS *Chimarra* Stephens is represented in all faunal regions of the world and contains a large number of species, most of which are tropical or warm-temperate in distribution (Wiggins 1977). Four species have been recorded from Australia; descriptions of the males of three of these and the female of the fourth were given by Mosely & Kimmins (1953). In reference to *C. australis* Navás, described from the female, Kimmins stated that he was "unable to recognize this species from the description" (Mosely & Kimmins 1953: 404); the whereabouts of the holotype are unknown (Neboiss 1988).

Chimarra is apparently diverse in northern Australia, with numerous undescribed species in collections, but *C. australica* (Ulmer) and *C. monticola* Kimmins are the only species known to occur in Victoria (Neboiss, pers. comm.). Males and females of both of these species have been bred out, and the larvae and pupae are described below. Larvae of overseas *Chimarra* have been described by various authors including Barnard (1934), Ross (1944), Marlier (1964), Hickin (1967), Lepneva (1970) and Wiggins (1977), although both Hickin and Lepneva based their descriptions on an earlier account by Marlier (1943). Barnard (1934), Ross (1944) and Lepneva (1970) also described pupae of *Chimarra*. Few female *Chimarra* have been described (Ross 1944, 1948, Kimmins 1957, Schmid 1982). Published information on immature specimens of Australian *Chimarra* is restricted to a key to Victorian genera of Philopotamidae (Cartwright & Dean 1982), general comments on the family by Riek (1970), a de-

scription of the larva of an unidentified species of *Chimarra* from New South Wales (incorrectly associated and identified as *Hydrobiosella letti* Korboot) by Korboot (1964), an investigation of the life cycle of *C. monticola* (Dean & Cartwright 1987), and an examination of the digestive tract contents of an unnamed species of *Chimarra* from Victoria (Chessman 1986).

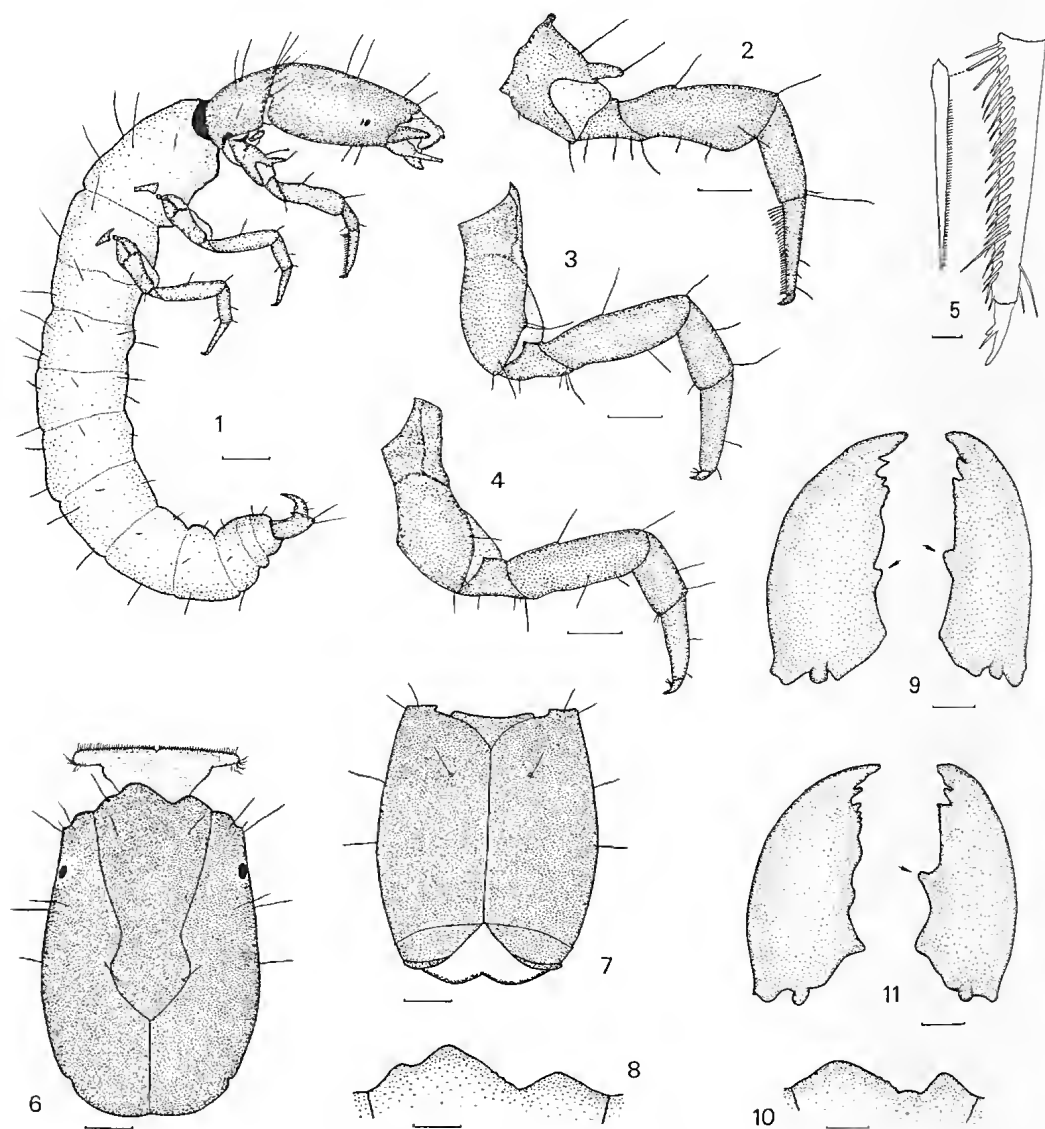
METHODS

Information on the distribution of *Chimarra* species in Victoria has been derived from extensive collecting of larvae over many years, supplemented by locality records of adult specimens held in the collections of the Museum of Victoria, Melbourne.

The life history of *Chimarra australica* was studied at a site on the Yarra River at Peninsula Road, approximately 80 km east of Melbourne and about 8 km downstream from the Upper Yarra Dam. The river at the study site is a fifth order stream but with reduced flow due to water abstraction upstream. Between August 1978 and February 1980, 12 samples were taken from a variety of habitats by a kick-sampling technique using a rectangular hand net (350 mm wide, mesh aperture size of 500 µm). Water temperature was measured at the time of sampling and ranged from 7.4°C (August) to 16.7°C (March). Stream discharge was measured at a site 1.5 km downstream of the sampling site. Total flow for the period January to September inclusive was 26,000 ML in 1978 and 8,000 ML in 1979 (MMBW Hydrographic Section records).

Larvae for life history determinations were examined under a stereomicroscope at $\times 50$ magnification; headwidth (to the nearest 0.02 mm) was measured. Larvae and pupae were collected by hand in order to rear adults for identification and to obtain information on the larval

capture net. Capture net dimensions were measured using a compound microscope at $\times 1000$ magnification. Female genitalia were drawn from cleared specimens, macerated in 10% KOH and transferred to glycerol for drawing.



Figs 1-11. Larvae of *Chimarra* Stevens. 1-9, *Chimarra monticola* Kimmins. 1, whole animal, scale = 0.5 mm. 2, foreleg, scale = 0.2 mm. 3, midleg, scale = 0.2 mm. 4, hindleg, scale = 0.2 mm. 5, tarsus of foreleg, detail of ventral seta, scale = 0.05 mm. 6, head including labrum, dorsal view, scale = 0.2 mm. 7, head, ventral view, scale = 0.2 mm. 8, anterior margin of frontoclypeal apotome, dorsal view, scale = 0.1 mm. 9, mandibles, ventral view, scale = 0.1 mm. 10-11, *Chimarra australica* (Ulmer). 10, anterior margin of frontoclypeal apotome, dorsal view, scale = 0.1 mm. 11, mandibles, ventral view, scale = 0.1 mm.

TAXONOMY

Chimarra Stephens

Figs 1–18

Final instar larva (Figs 1–11)

Diagnosis. (Modified after Ross 1944: 48–51, Lepneva 1970: 421–422, Wiggins 1977: 312–313.) Length 8–12 mm (\bar{x} = 9.7 mm, n = 24). Larvae campodeiform. Head and pronotum sclerotized, orange-brown in colour. Mesonotum and metanotum not sclerotized. Abdomen white or yellow, abdominal gills absent (Fig. 1). Labrum membranous, brushlike, anterior margin broader than posterior margin. Frontoclypeal apotome narrow, constricted in posterior half. Anterior margin of frontoclypeal apotome with prominent asymmetrical notch (Figs 6, 8, 10). Ventral surface of head with seta number 18 located on anterior third of head capsule, transverse sulcus or ridge adjacent to occipital margin (Fig. 7). Thoracic legs simple, tarsus approximately same length as tibia, tarsal claw short and stout (Figs 2, 3, 4). Tarsus of foreleg with ventral row of setae, each seta with fringe of spinules on

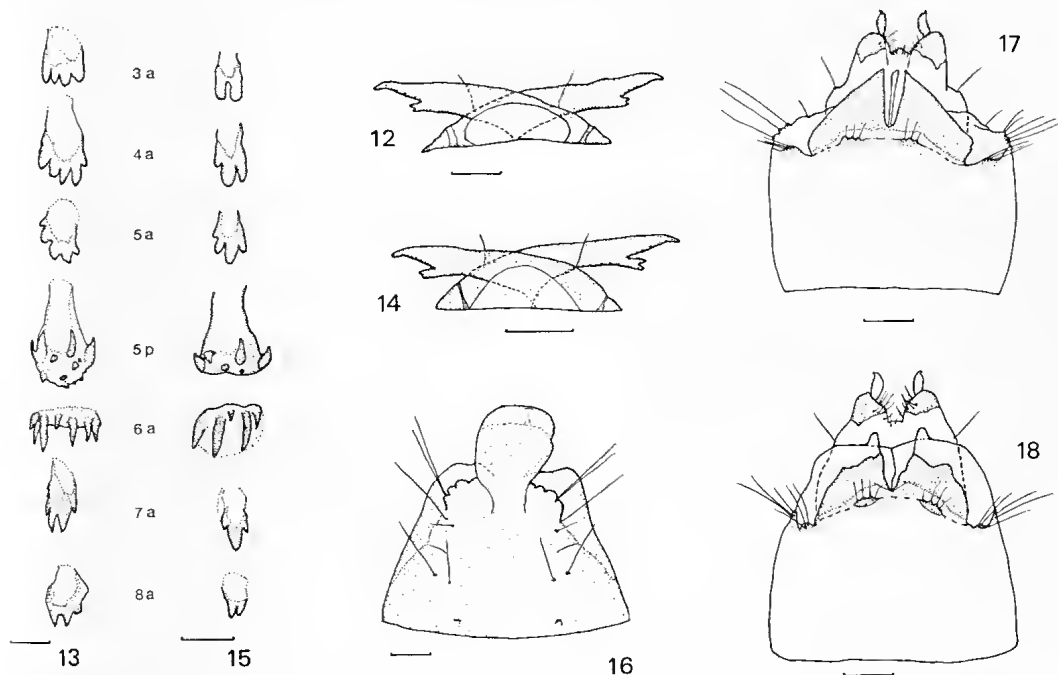
anterior margin. Spinules about 1 μ m apart (Fig. 5). Dorsal surface of forecoxa with a seta mesially, sclerotized process bearing a terminal seta distally (Fig. 2).

Pupa (Figs 12–16)

Diagnosis. (Modified after Lepneva 1970: 421–422.) Length 5.6–8.2 mm (\bar{x} = 6.7 mm, n = 5). Labrum broadly rounded. Mandibles dark reddish-brown, curved near base, apices pointed with prominent bifid subapical tooth-like process (Figs 12, 14). Tibial spurs 1:4:4. Anterior hook plates present on abdominal segments 3–8, posterior hook plates present on segment 5 only (Figs 13, 15). Abdomen without gills or lateral fringe of setae. Apex of abdomen without paired anal processes (Fig. 16).

Female (Figs 17, 18)

Diagnosis. (Modified after Mosely & Kimmins 1953, Kimmins 1957, Schmid 1982.) Ocelli present. Maxillary palpi five-segmented, segment 5 long and flexible. Spurs 1:4:4. Anterior wings with R1 simple, apical forks 1, 2, 3 and 5 present;



Figs 12–18. Pupae and females of *Chimarra* Stephens. 12, 13, *Chimarra monticola* Kimmins pupa. 12, mandibles and labrum, dorsal view, scale = 0.2 mm. 13, hook plates, dorsal view, scale = 0.05 mm. 14–16, *Chimarra australica* (Ulmer) pupa. 14, mandibles and labrum, dorsal view, scale = 0.2 mm. 15, hook plates, dorsal view, scale = 0.05 mm. 16, tip of abdomen, dorsal view, scale = 0.1 mm. 17, *Chimarra monticola* Kimmins, female genitalia, ventral view, scale = 0.1 mm. 18, *Chimarra australica* (Ulmer), female genitalia, ventral view, scale = 0.1 mm.

Key to Victorian species of *Chimarra* Stephens

Larvae

1. Frontoclypeal notch V-shaped (Fig. 8, ∇); projection on inner margin of basal half of both mandibles (Fig. 9, ∇) *C. monticola* Kimmins
 — Frontoclypeal notch with flattened base (Fig. 10, ∇); projection on inner margin of basal half of left mandible only (Fig. 11, ∇) *C. australica* (Ulmer)

Pupae

1. Hook plates on segment 3 and 4 with 4–6 large teeth (Fig. 13) *C. monticola* Kimmins
 — Hook plates on segments 3 and 4 with 2 or 3 large teeth (Fig. 15) ... *C. australica* (Ulmer)

Adult females

1. Ninth sternite with 2 triangular sclerites (Fig. 17) *C. monticola* Kimmins
 — Ninth sternite with 2 sub-trapezoidal sclerites (Fig. 18) *C. australica* (Ulmer)

Adult males

1. Apices of parameres forming upturned hook on each side of penis (Mosely & Kimmins 1953, fig. 274; Neboiss 1986: 105) *C. australica* (Ulmer)
 — Apices of parameres triangular, not hooked (Mosely & Kimmins 1953, fig. 275; Neboiss 1986: 105) *C. monticola* Kimmins

posterior wings with forks 2, 3 and 5 present; discoidal cell present in both wings. Female abdomen terminates bluntly, segments 9 and 10 short.

Chimarra monticola Kimmins

Figs 1–9, 12, 13, 17

Chimarra monticola Kimmins in Mosely & Kimmins 1953: 402–403, fig. 275.

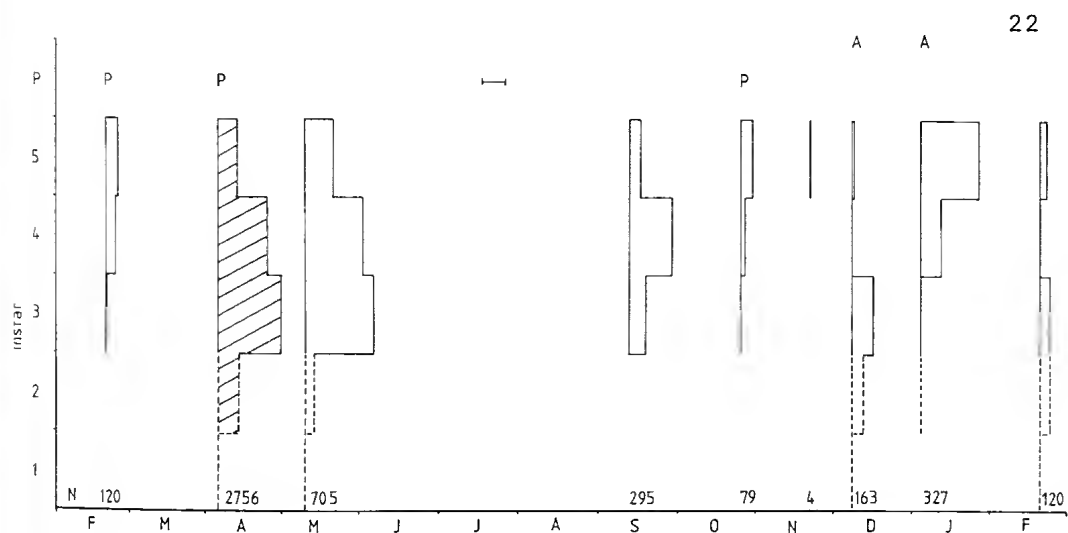
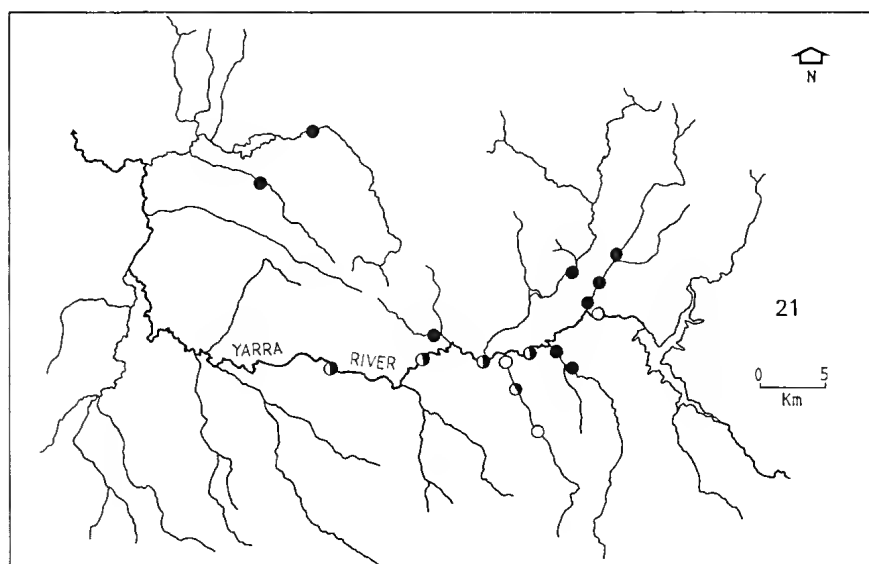
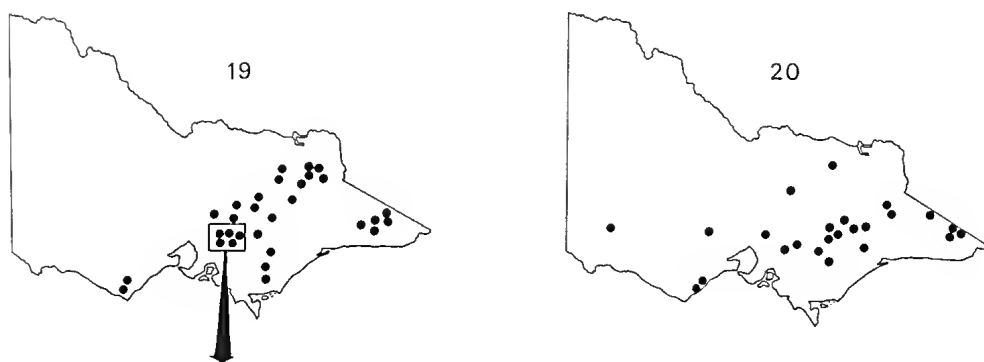
Diagnosis

Final instar larva. (Figs 1–9.) Length 8.3–11.7

mm (\bar{x} = 10.1, n = 12). Head length about 1.5 × width (Fig. 6). Frontoclypeal notch V-shaped. Left margin of frontoclypeus projecting farther than right (Fig. 8). Both mandibles with small projection on inner margin mesially (Fig. 9).

Pupa. (Figs 12, 13.) Length 6.3–8.2 mm (\bar{x} = 7.2 mm, n = 3). Mandibles with short, bifid sub-apical process (Fig. 12), slightly less conspicuous than in *C. australica*. Anterior hook plates on abdominal segment 3 usually with 4 teeth, segment 4 with 5 or 6 teeth (Fig. 13); generally with more teeth on each hook plate than on corresponding plate on *C. australica*.

Figs 19–22. 19, distribution of *Chimarra monticola* Kimmins in Victoria. 20, distribution of *Chimarra australica* (Ulmer) in Victoria. 21, distribution of *Chimarra* in the Yarra River system 50 km east of Melbourne: ● = *C. monticola* Kimmins recorded, ○ = *C. australica* (Ulmer) recorded, ◐ = both *Chimarra* species recorded. 22, seasonal abundance of instars of *Chimarra australica* (Ulmer) in the Yarra River, Peninsula Road, 1979–80: scale = 100 individuals for open histograms, 420 individuals for cross-hatched histogram; N = number of specimens collected on each sampling trip; P = prepupae and pupae recorded; A = adults collected; all *Chimarra* instars 1 and 2 have been included in the figure although a small proportion may have been *C. monticola*.



Female. (Fig. 17.) Black; wing venation as for male. Anterior wing length 5.6–8.6 mm (\bar{x} = 7.2, n = 12). Female genitalia with eighth tergite and sternite entirely fused, apical margin fringed laterally with long setae. Ninth tergite arched; sternite with two triangular sclerites, their inner margins touching at base. Tenth segment with a pair of short, single-segmented cerci.

Chimarra australica (Ulmer)

Figs 10, 11, 14–16, 18

Chimarra australica Ulmer 1916: 3–5, figs 3–6.—
Mosely & Kimmins 1953: 399–402, fig. 274.

Diagnosis

Final instar larva. (Figs 10, 11.) Length 8.3–10.4 mm (\bar{x} = 9.2 mm, n = 12). Head length about 1.5 × width. Frontoclypeal notch with flattened base (Fig. 10). Only left mandible with projection on mesal margin near middle (Fig. 11).

Pupa. (Figs 14–16.) Length 5.6–6.5 mm (\bar{x} = 6.0, n = 2). Mandibles with bifid, subapical process (Fig. 14), slightly more conspicuous than in *C. monticola*. Anterior hook plates on abdominal segment 3 with 2 or 3 teeth, segment 4 with 3 or 4 teeth (Fig. 15); generally with fewer teeth on each hook plate than on corresponding plate of *C. monticola*.

Female. (Fig. 18.) Black; wing venation as for male. Anterior wing length 5.3–6.4 mm (\bar{x} = 5.7 mm, n = 15). Female genitalia with eighth tergite and sternite entirely fused, apical margin fringed laterally with long setae. Ninth tergite arched; sternite with two sub-trapezoidal sclerites, their inner margins touching at base. Tenth segment with a pair of short, single-segmented cerci.

DISTRIBUTION IN VICTORIA

C. monticola is widely distributed in eastern Victoria, with records including high altitude streams on the Bogong High Plains and around Mount Buller. The only record from west of Melbourne is from the Otway Ranges (Fig. 19).

C. australica is also widespread in eastern Victoria but there are no records from high altitude streams, and the species is generally found in warmer streams than *C. monticola*. In western Victoria, *C. australica* has been recorded from the Wannon River, Lal Lal Falls and the Otway Ranges (Fig. 20).

Extensive collecting in the Yarra River system over several years has provided reasonably complete distributional data for that area (Fig. 21). *Chimarra* has not been recorded from first or second order streams, occurs in some third order streams, but appears to be more common in larger streams of order four or higher. *C. australica* has been collected from the mainstream of the Yarra River and Starvation Creek at several sites below a small weir. *C. monticola* is widely distributed in larger tributaries but has been recorded at four sites in the Yarra River mainstream where the two species overlap. *C. monticola* is, however, usually quite rare in mainstream samples where *C. australica* is always dominant.

BIOLOGY

Headwidths of larval instars of both species collected from the Yarra River at Peninsula Road during 1979–80, together with those of *C. monticola* collected from the O'Shannassy River in 1975–77 (from Dean & Cartwright 1987), are presented in Table 1. Instars 1 and 2 from the Yarra River could not be identified positively but, given the dominance of *C. australica* in later instars, most of the early instars probably also belonged to that species.

	1	2	INSTAR 3	4	5
O'Shannassy R. <i>C. monticola</i>	—	0.26–0.28	0.38–0.50	0.58–0.72	0.82–1.12
Yarra R. <i>C. monticola</i>	—	—	0.46–0.48	0.58–0.70	0.80–1.00
<i>C. australica</i>	—	—	0.34–0.46	0.48–0.66	0.70–0.92
<i>Chimarra</i> sp.	0.14	0.24–0.26	—	—	—

Table 1. Headwidth range (mm) of larval instars of *Chimarra monticola* Kimmins from the O'Shannassy River (Dean & Cartwright 1987) and *C. monticola* and *C. australica* (Ulmer) from the Yarra River 1979–80.

Based on instars 3–5 only, numbers of *C. monticola* in the Yarra River were typically low (less than 10% of the *Chimarra* individuals in each sample collected during 1979–80), although in samples collected in August and October of 1978, *C. monticola* comprised 29% and 25% of the total *Chimarra* numbers respectively.

Size distributions of instars of *C. australica* in the Yarra River samples during 1979–80 are illustrated in Fig. 22. The life cycle is difficult to interpret due to the absence of samples in some months, and the wide range of instars at certain times of the year. Instar 1 and 2 larvae were collected in April and May of 1979, and probably overwintered mainly as instars 3–5 and pupated during October–November. Instars 1 and 2 appeared in samples again in December and January, and probably grew rapidly to pupate in late summer–early autumn. Pupae were collected in February, April and October. With early instars present in autumn and summer, and pupae in late spring and late summer–autumn, the life cycle appears to be bivoltine, although poorly synchronized.

Capture nets of *C. australica* final instar larvae from the Yarra River had mesh openings of 1.1–1.2 μm by 2.1–14.6 μm . *C. monticola* in the O'Shannassy River had capture nets with mesh openings of 0.9–1.2 μm by 5.5–18.0 μm .

DISCUSSION

The two Victorian species of *Chimarra* can be distinguished by small but reliable characters: the shape of the anterior margin of the frontoclypeus and mandibles in final instar larvae; the number of teeth on the abdominal hook plates in pupae; and the shape of the distal sclerites attached to the ninth abdominal sternite of females. The shapes of both the frontoclypeal notch and the mesal margin of the mandibles have previously been used to distinguish larvae of *Chimarra* species in North America (Ross 1944) and South America (Marlier 1964). In pupae, there is some variability in the number of teeth on the hook plates of most segments, and this variability has also been reported by Lepneva (1970). This character should be used with some caution, although it has been found reliable in material examined in the present study.

The life cycle of *C. australica* in the Yarra River is poorly synchronized and apparently bivoltine. This contrasts with the life cycle of *C. monticola*, which was reported by Dean & Cartwright (1987) to be well synchronized and

univoltine. These differences can be explained by the higher water temperatures recorded in the Yarra River. Similar differences have been reported from the northern hemisphere, with bivoltinism being reported in species of *Chimarra* in Georgia (USA) by Cudney & Wallace (1980), in Virginia by Parker & Voshell (1982), in Quebec by Morin & Harper (1986), and in South Carolina by Smock (1988). Univoltinism has been documented in *C. atterrима* Hagen in Illinois by Ross (1944) and in Ontario by Williams & Hynes (1973).

Although *C. australica* was always dominant in the Yarra River during the study period, the proportion of *C. monticola* was higher in August and October of 1978 (25–30% of *Chimarra* individuals collected) than in 1979 (less than 10% of *Chimarra* in each sample). The higher proportion of *C. monticola* in 1978 may have been related to the much higher water flow in that year.

Nets of *Chimarra* species have been little studied. Wallace & Malas (1976) found that final instar larvae of *C. socia*? in North America produce nets with mesh openings ranging from 0.8 \times 3 to 0.8 \times 9 μm . In comparison with these sizes, the mesh openings of final instar larvae of the two Victorian species were slightly greater in width and extremely variable in length.

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TERTIARY PROTEACEAE IN AUSTRALIA: A RE-INVESTIGATION OF *BANKSIA ADUNCA* AND *DRYANDRA URNIFORMIS*

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HILL, ROBERT S., 1990:05:31. Tertiary Proteaceae in Australia: a re-investigation of *Banksia adunca* and *Dryandra urniformis*. *Proceedings of the Royal Society of Victoria* 102 (1): 23–28. ISSN 0035-9211.

The specimens described by Deane (1925) as *Banksia adunca* and *Dryandra urniformis* from Upper Oligocene–Lower Miocene coals at Morwell, Victoria have been re-examined and their cuticular morphology examined for the first time. *Banksia adunca* is considered to be conspecific with *Banksiaephyllum fastigiatum* (Deane) Cookson & Duigan. *D. urniformis* is also transferred to *Banksiaephyllum* and is considered to be closely related to *B. elongatum* Hill & Christophel, 1988 from the Upper Oligocene–Lower Miocene at Loy Yang. These *Banksiaephyllum* species are particularly important in tracing the history of the development of sclerophylly and xeromorphy in Australian plants.

MACROFOSSILS of the Proteaceae are well represented in Australian Tertiary sediments, leaves and reproductive structures of a range of genera having been described (Cookson & Duigan 1950, Pike 1953, Lange 1978, Blackburn 1981, McNamara & Scott 1983, Christophel 1984, Carpenter & Hill 1988, Hill & Christophel 1988). Amongst the Proteaceae the most common and diverse macrofossils belong to the tribe Banksieae.

The coals of the Latrobe Valley in Gippsland, Victoria contain a diversity of macrofossils in the Banksieae, nine species based on vegetative material having been described by Deane (1925), Cookson & Duigan (1950) and Hill & Christophel (1988). Following Ettingshausen (1888), Deane (1925) adopted the convention of placing serrate leaves in *Banksia* and pinnate leaves in *Dryandra* but he was aware that this distinction is invalid amongst living species. Cookson & Duigan (1950) concluded that extant species of these two genera cannot be separated on leaf form alone and thus erected the form genus *Banksiaephyllum* for fossil leaves with the characteristics of *Banksia* and/or *Dryandra*. They transferred *Banksia fastigata* Deane to *Banksiaephyllum* on the basis of the original specimen and new collections. The other two species described by Deane, *Banksia adunca* and *Dryandra urniformis*, were listed by Cookson & Duigan amongst species requiring re-investigation to establish their affinities. Hill & Christophel (1988) noted that leaves should not be placed in *Banksiaephyllum* unless the cuticular morphology was sufficiently well preserved to support the assignment.

The type specimens of *Banksia adunca* and *Dryandra urniformis* were examined recently in the Museum of Victoria (specimen numbers with prefix NMV), and it was determined that in both specimens the cuticle was preserved. The specimens have been re-investigated and their cuticular morphology studied to determine whether their placement in the tribe Banksieae is valid, and if so whether they should be transferred to the form genus *Banksiaephyllum*. Both fossil species were collected from the Morwell coal (Deane 1925) which spans the Upper Oligocene to Lower Miocene (Stover & Partridge 1973), but the precise horizon from which the specimens came is uncertain.

MATERIAL AND METHODS

The material of each species consists of only part of the leaf. Extreme care was required in preparing the cuticle since only a small amount of leaf tissue is available. Before any attempt was made to remove leaf fragments, the specimens were photographed using an Olympus OM-4 camera with bellows and reflected light. Both leaves appear to have been coated with some type of varnish for protection, and this was successfully removed by soaking small fragments of the leaves in acetone for several hours. Following this treatment the leaf fragments were placed in 10% chromic acid until the internal leaf tissue had dissolved. The cuticular fragments were then washed, neutralised in 5% ammonia, stained in 1% aqueous safranin O, and mounted on microscope slides in phenol glycerine jelly. Cuticles were examined using a Zeiss Axioskop compound microscope.

Both specimens yielded well preserved cuticle, although the stomatiferous surface of *Banksia adnca* could not be cleaned completely despite a number of attempts. It is possible that other methods may be successful in cleaning this cuticle, but given the small amount available it was considered that the risk of damaging the cuticle was too great to persevere.

Both species clearly belong to the tribe Banksieae of the Proteaceae. They contain a combination of characters listed by Cookson & Duigan (1950) and Hill & Christophel (1988) as being typical of the tribe (stomata with paired subsidiary cells parallel to the pore (brachyparacytic), serrations with prominent veins ending in the apices, and distinctive trichome types). Like other fossil leaves of this type, however, they cannot be placed with certainty in either *Banksia* or *Dryandra*, and so must be transferred to the form genus *Banksieaephyllum*.

TAXONOMIC DESCRIPTIONS

Family PROTEACEAE
Subfamily GREVILLIOIDEAE
Tribe BANKSIEAE

Genus *Banksieaephyllum* Cookson & Duigan

Banksieaephyllum urniforme (Deane) Hill,
comb. nov.

Figs 1A–D, 2A

Dryandra urniformis Deane 1925: 495, pl. 62,
fig. 9.

Holotype. NMV P15127.

Emended diagnosis. Leaves bilateral, at least 6 mm wide, pinnately lobed. Lobes acute and apically directed; apical and basal sides of lobes convex, apical side much shorter than basal side. Leaf base and apex unknown. Secondary venation pattern craspedodromous, with a number of secondary veins per lobe. Stomata brachyparacytic, superficial. Trichome bases of two types abundant on stomatiferous epidermis. Large trichome bases usually associated with one but sometimes with two or three epidermal cells; trichome small, unicellular. Small trichome bases associated with one epidermal cell; trichome basal cell thickly cutinized, cylindrical; apical cell(s) not preserved. Trichome bases absent from upper epidermis.

Discussion. This species is represented by only a fragment of a single leaf but the cuticle is well preserved. The leaf has characteristic urn-shaped pinnae which are similar to those described in *Banksieaephyllum elongatum* Hill & Christophel (1988). Hill & Christophel (1988) commented on this similarity but considered the pinnae of *B. urniforme* and *B. elongatum* to be consistently of a different shape. The specimen of *B. urniforme* was not studied by Hill & Christophel, however, and its cuticular morphology was therefore not considered. The cuticle of *B. urniforme* is similar to that of *B. elongatum* but differs from it most notably in lacking small, simple trichome bases on the upper epidermis.

The remaining fossil species of Banksieae with pinnate leaves are much larger in size than *Banksieaephyllum urniforme*, and have very distinct cuticular patterns (*Banksieaephyllum cuneatum* Hill & Christophel, 1988 and *B. incisum* Blackburn, 1981), distinctive leaf bases (*Banksieaephyllumis decurrens* Hill & Christophel, 1988), or distinctively rounded pinnae (*Banksieaephyllum pinnatum* Cookson & Duigan, 1950).

Banksieaephyllum elongatum Hill &
Christophel, 1988

Banksieaephyllum elongatus Hill & Christophel
1988: 212–214, figs 24–29.

Emended diagnosis. Leaves bilateral, at least 60 mm long and up to 10 mm wide, pinnately lobed. Lobes acute and apically directed; apical side of lobe usually straight or slightly concave, much shorter than basal side; basal side convex. Leaf base cuneate, apex unknown. Secondary venation pattern craspedodromous, with a variable number of secondary veins per lobe. Stomata brachyparacytic, superficial. Trichome bases of two types abundant on stomatiferous epidermis. Large trichome bases usually associated with one but sometimes with two or three epidermal cells; trichome small, unicellular. Small trichome bases associated with one epidermal cell; trichome basal cell thickly cutinized, cylindrical; apical cell(s) not preserved. Small, unicellular trichome foot cells scattered on upper epidermis; trichomes unknown.

Discussion. An emended diagnosis of *B. elongatum* is given here because in the original diagnosis the small unicellular trichome bases on the upper epidermis were not included. This is one

of the most important characters separating this species from *B. urniforme*.

***Banksiaephyllum fastigatum* (Deane) Cookson & Duigan**

Figs 1E–H, 2B

Banksia fastigata Deane 1925: 494, text-fig. 140, pl. 61, figs 1, 4, pl. 62, figs 6, 7?, pl. 63, fig. 13.

Banksia adunca Deane 1925: 494–5, text-fig. 141, pl. 62, fig. 10, pl. 64, fig. 18.

Banksiaephyllum fastigatum.—Cookson & Duigan 1950: 153, pl. 6, figs 43–48.

Holotype of *Banksia adunca*. NMV P15128.

Emended diagnosis. Leaves long, regularly serrate, about 15 mm wide and tapering at both base and apex. Serrations curved towards apex of leaf; sinuses about 1/3 width from midvein to apex of serration. Secondary veins upwardly curved, with one terminating in each serration and one near each sinus. Cuticular pattern suggests that areoles are well-developed. Stomata situated in slight depressions, long axes of which tend to be oriented in one direction. Individual stomata appear to be slightly sunken below surface of surrounding epidermis. Lying parallel to pore of each stoma are two inconspicuous subsidiary cells, over which neighbouring epidermal cells may project slightly. Stomatal apparatus surrounded by 3–6 narrow cells which stain deeply. Epidermal parenchyma not uniform; most of its cells of medium size, with straight or curved, very thin and pitted walls in stomatal areas, and similar but somewhat thicker walls above veins. Amongst cells of parenchyma are scattered exceptionally small cells 4–6 µm in diameter, supporting hair bases of similar size. Cells over midvein small, square to quadrangular, with moderately thick, unpitted walls; small hair bases sparsely developed. Cuticle longitudinally ridged. Upper epidermal cells above veins somewhat smaller than those of areas enclosed by veins; all have rather thin, unpitted, straight or slightly curved walls.

Discussion. *Banksia adunca* is distinct from 10 of the 13 previously described fossil species, which either have entire leaf margins (*Banksiaephyllum acuminatum* Cookson & Duigan, 1950, *B. laeve* Cookson & Duigan, 1950 and *B. obovatum* Cookson & Duigan, 1950), leaves that are divided into the midvein (*Banksiaephyllum cuneatum*, *B. incisum*, *B. elongatum*, *B. pinnatum* and *Banksiaeformis decurrens*), or leaves

that are serrate with more than one secondary vein per serration (*Banksiaephyllum regulare* Hill & Christophel, 1988 and *B. angustum* Cookson & Duigan, 1950).

Banksia adunca is similar in leaf morphology and venation pattern to *Banksiaephyllum attenuatum* Hill & Christophel, 1988, *B. fastigatum* and *Banksiaeformis dentatus* Hill & Christophel (1988). The comparison with *B. dentatus* can be carried no further, since this species is not organically preserved (and hence is placed in a separate genus). Hill & Christophel (1988) noted the similarity between *Banksiaephyllum attenuatum* and *B. fastigatum*, with the major difference being the superficial stomates in the former in comparison with the sunken stomates in the latter. In this and all other features observed, *Banksia adunca* is very similar to *Banksiaephyllum fastigatum* and its cuticular morphology is identical. Deane (1925) described differences in serration morphology but differences such as these commonly occur within extant species. It is concluded, therefore, that *Banksia adunca* and *Banksiaephyllum fastigatum* are synonymous. The name *Banksiaephyllum fastigatum* is retained for the species because this name was used by Cookson & Duigan (1950) and more recent authors (e.g. Blackburn 1981, Hill & Christophel 1988), and its continued use will avoid confusion for future workers. Since *Banksia fastigata* and *B. adunca* were described in the same paper, the choice is one of convenience since neither name has priority.

The diagnosis of *B. fastigatum* provided by Cookson & Duigan (1950) has been emended to accommodate the slightly different shape of the serrations in the holotype of *Banksia adunca*.

DISCUSSION

The coals of the Latrobe Valley have yielded eight species of *Banksiaephyllum*, three of them (*B. laeve*, *B. obovatum* and *B. pinnatum*) being widespread and relatively common in both the Yallourn and Morwell coal (Blackburn 1985), the others occurring infrequently and in some cases being known only from single specimens. It is clear, however, that this group was an important part of the vegetation which contributed to coal formation, and a study of the leaf form of these species is of major importance in understanding the environmental conditions under which the plants were growing.

The leaves of all these species are relatively sclerophyllous in nature, a condition which is a

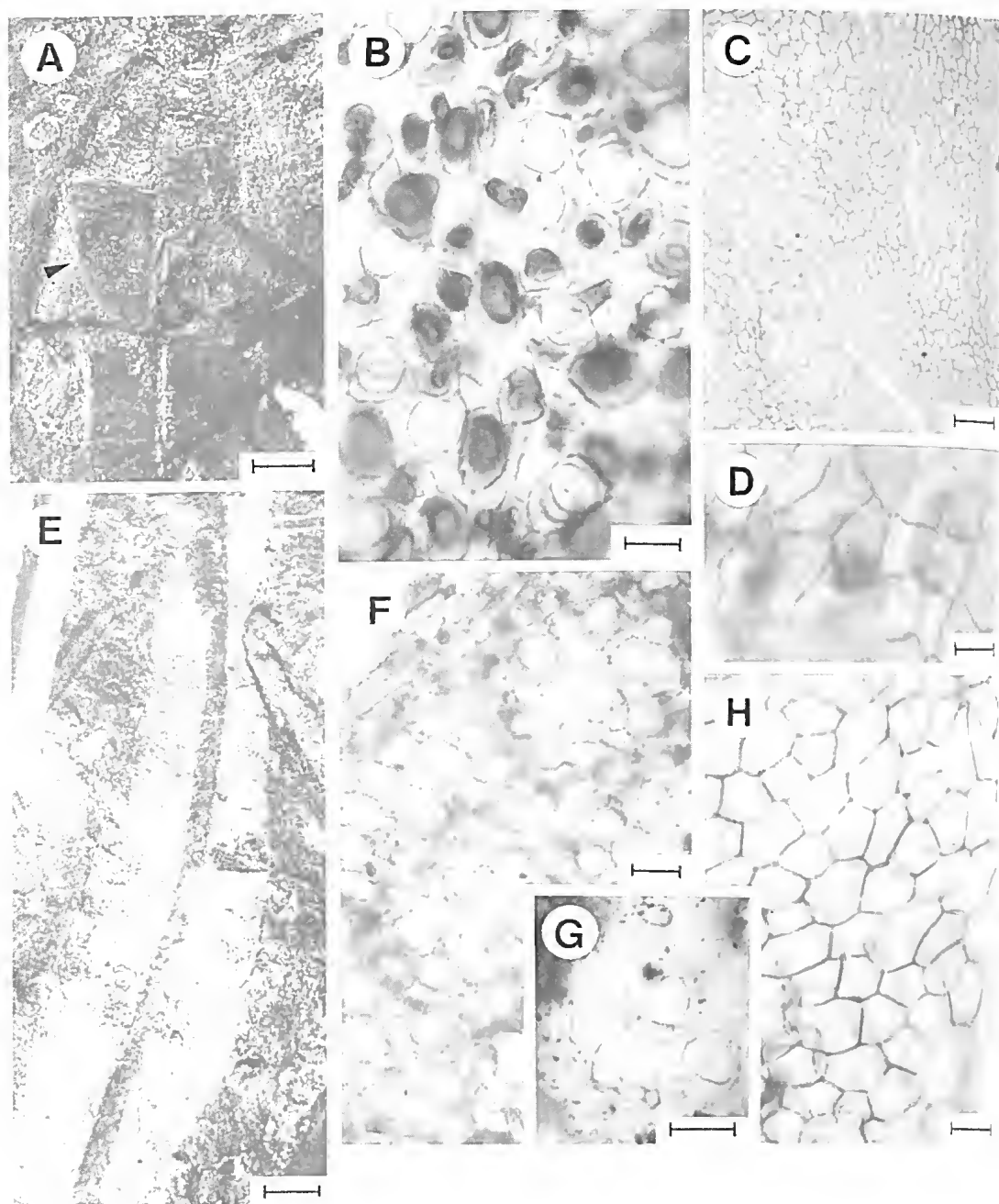


Fig. 1. A-D, *Banksiaephyllum urniforme*, holotype, NMV P15127. A, entire specimen; note single well-preserved lobe of leaf (arrowed); scale = 2 mm. B, lower epidermis showing stomates and two common trichome base types; scale = 25 μ m. C, upper epidermis; note absence of trichomes; scale = 100 μ m. D, two multicellular trichome bases near leaf margin; these bases are characteristic of Proteaceae; scale = 25 μ m. E-H, *Banksiaephyllum fastigatum*, NMV P15128, holotype of *Banksia adunca*. E, entire leaf; scale = 2 mm. F, lower epidermis; cuticle is not completely clean but it can be seen that trichome bases are lacking; scale = 25 μ m. G, lower epidermis; stomates with small brachyparacytic subsidiary cells visible; scale = 25 μ m. H, upper epidermis; scale = 25 μ m.

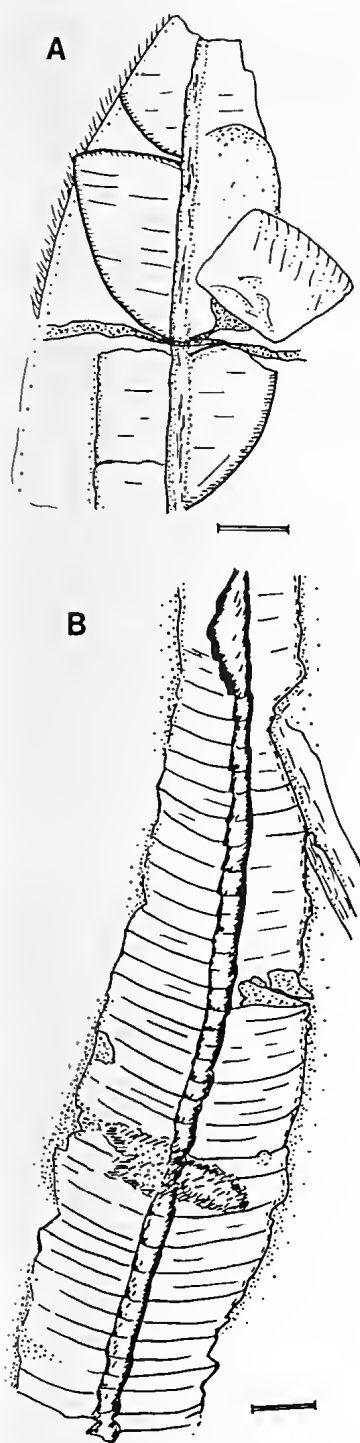


Fig. 2 A, drawing of holotype of *Banksiaephyllum urniforme*, NMV P15127, see Fig. 1A; scale = 2 mm. B, drawing of specimen of *B. fastigiatum* shown in Fig. 1E, NMV P15128; scale = 2 mm.

response to low nutrient levels in the soil, particularly low phosphorus (Beadle 1966). There has often been confusion about the interaction of nutrient levels and climate (in particular low rainfall) as contributing factors to sclerophylly. Many sclerophyllous characters are also useful xeromorphic adaptations (e.g. small leaf size, thick cuticle), and with features such as these it is difficult if not impossible to determine whether low nutrients or a dry climate was the causal factor. There are some leaf characters, however, which can be described as xeromorphic and are distinct from scleromorphy. Most prominent amongst these are adaptations directed towards protecting the stomates, so that the boundary layer resistance is increased (e.g. sunken stomates, stomates in pits, revolute leaf margins, hairs around the stomates, etc.). It is the presence or absence of these characters which should allow an interpretation of the factor(s) most affecting leaf form in *Banksiaephyllum* (Hill in press).

Although all species of *Banksiaephyllum* described from the Latrobe Valley coal are sclerophyllous, only some have adaptations which can be considered as solely xeromorphic. *B. angustum* and *B. acuminatum* are the most xeromorphic species, having strongly recurved leaf margins, stomata sunken in pits, and very hairy stomatal leaf surfaces. Blackburn (1985) noted these xeromorphic features and their relationship to the darker coals which accumulated in the drier environments. Some of the other species (e.g. *B. laevis*, *B. obovatum*) exhibit almost no xeromorphic adaptations, and the remaining species are intermediate in form. Even the most xeromorphic species are not as strongly adapted to preventing water loss as are some of the extant *Banksia* and *Dryandra* species, and they may be in a transitional state towards this development. Thus it can be concluded that these fossils offer the earliest fossil evidence of xeromorphy in Australia, even though *Banksiaephyllum* is recorded from the Palaeocene onwards. This suggests that these coal floras are an important site for the study of the way in which the morphological adaptations to the Mediterranean climate evolved in Australia. Future studies on other taxonomic groups should refine these conclusions.

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DISTRIBUTION OF FRESHWATER FISH IN THE OTWAY REGION, SOUTH-WESTERN VICTORIA

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The distribution of freshwater fishes in the Otway region of south-western Victoria was determined from surveys carried out at 53 sites between 1982 and 1988. Eighteen fish species (14 native and 4 introduced) were recorded. The distribution of native fish appears to be related to geomorphological conditions that existed during and after the last glaciation 20,000-5,000 years ago. The short coastal streams east of Cape Otway may have formed after the Bass Strait land bridge was submerged, or may have been subjected to desiccation during an ensuing drier period. The native fish fauna of these streams consists of species with marine phases in their lifecycles and may have originated by recolonization from the sea. Although species with entirely freshwater lifecycles are absent from these streams, they are abundant in the Barwon, Aire and Gellibrand river systems, suggesting that these systems were less affected by geomorphological conditions due to their much greater size or to their location.

Australian grayling were collected from nine sites in the Otway coastal streams, and valuable populations of freshwater blackfish and of several species of Galaxiidae were also recorded. The discovery of a Tasmanian mudfish in Wye River provides a second location for this species in Victoria, and whitebait of Australian grayling were recorded from the Cumberland River. Brown trout were found to be widespread but other introduced species were rare in the coastal streams. The freshwater fish faunas of the Otway region and of northern Tasmania are compared. The importance of the Otway region in the conservation of native freshwater fish species is discussed and careful management is recommended.

THE FISH fauna of the Otway region (Fig. 1) of south-western Victoria, which forms part of the study area for the south-western regional water strategy plan (Natural Resources & Environment Committee 1984), has not been surveyed since the mid-1960s (Renowden 1968). Most of the recent faunal surveys conducted in the region (Emison et al. 1975, Bennett 1982, Pescott 1982, Conole & Baverstock 1983, 1985, King 1986, Wallis 1986, Earl & Bennett 1986) were primarily concerned with terrestrial vertebrates and gathered few or no data on fishes.

Here we report on recent surveys of freshwater fishes conducted at 53 sites in the Otway region. We compare the freshwater fish fauna of the coastal Otway streams with those of the larger river systems such as the Barwon and Gellibrand, and relate the distribution of the species to the geomorphological history of the region, to the species' life cycles and to availability of habitat.

The fish faunas of the Gellibrand and Barwon Rivers have been recorded by Tunbridge & Glenane (1988) and by Hall & Tunbridge (1988) respectively. Some information on the estuarine

fish species of the region has been published by McCarraher (1986).

STUDY AREA

The Otway region is physiographically divided into the Otway Range and the coastal plains. The coastal plains, which are used primarily for agriculture, extend up to 50 km inland and are bounded to the north by volcanic plains. The Otway Range extends for almost 100 km from Aireys Inlet (38°28'S, 144°06'E) in the east to Moonlight Head (38°46'S, 143°14'E) in the west. The range is about 500 m high over most of its length, with Mount Cowley being the highest point at 670 m (Douglas 1975).

The wettest part of the region lies along the main ridge of the Otway Range where the mean annual rainfall is more than 1800 mm, and a marked rain shadow extends over much of the inland plains to the north-east (Lindforth 1975).

The two largest waterways in the region are the Barwon and Gellibrand Rivers which drain the northern slopes of the Otway Ranges and

have mean daily flows of 745 ML and 714 ML respectively (State Rivers & Water Supply Commission 1984). Both rivers have weirs on their upper reaches and have been the subject of stream-flow studies which provide recommended flow rates to maintain fish populations (Tunbridge & Glenane 1988, Tunbridge 1988). Both rivers have their headwaters in forested catchments but flow mostly through farmland. The lower reaches of the Barwon River flow through urban areas of the city of Geelong.

The Aire River system west of Cape Otway is the third largest waterway in the Otway region, the main river having a length of 40 km and a mean daily flow of 174 ML (State Rivers & Water Supply Commission 1984). Watercourses draining the main ridge east of Cape Otway are primarily short, fast-flowing streams emptying into the Southern Ocean. Many of these streams flow for less than 10 km and have mean flow rates of less than 60 ML per day. Many of them flow through forested catchments which remain in a relatively natural condition. Waterfalls are common on the coastal streams and often form natural barriers to fish passage.

Waters in the Otway region have been stocked with salmonids from as early as 1879, initially by the Geelong and Western District Fish Acclimatisation Society and later by Victorian Government departments (Barnham 1989). Most streams were stocked with brown trout, *Salmo trutta*, but rainbow trout, *Oncorhynchus mykiss*, were also released until 1968 at a smaller number of sites, including the West Barwon Dam and the lower reaches of the Barwon River (Wharton 1969). Only the Aire, Barham, Barwon, Ford, Gellibrand and St Georges (Reservoir Alledale) Rivers have been stocked with brown trout since 1970 (Barnham 1989). Between 1982 and 1986 the Barwon River was the only river stocked, receiving between 3000 and 5000 brown trout annually (Hume & Barnham 1986).

METHODS

The location of each site sampled is shown in Fig. 1. Map grid references for each site (obtained from 1:100,000 maps of the Topographic Survey National Map Series) as well as the names of streams and the dates and method of sampling are given in the Appendix.

A Smith Root MK VIA bank-mounted electrofisher (Koehn & McKenzie 1985) was used to sample fish at 52 sites. Jackson & Williams

(1980) sampled site 20 by electrofishing in 1974. Rotenone was used by McCarragher (1986) at site 4 in 1977 and 1981, and by Baxter (1985) to collect spotted galaxias and Australian grayling at site 26 on 1 March 1982. A dip net was used to sample whitebait at site numbers 6, 7, 11, 14, 18, 21, 25, 30, 33, 42 and 45 (Appendix). Two sites were also sampled overnight as follows:

Sites 36 and 37: 4 single winged fyke nets (13 mm mesh)

Site 37: 25 mm, 50 mm, 75 mm, 88 mm, 100 mm and 125 mm mesh nets, each 25 m long.

Electrofishing was considered to be efficient at all sites (see Koehn & McKenzie 1985) for all species except lamprey ammocoetes which often avoided capture by burrowing. Dip net sampling for whitebait of the common galaxias at site 45 was not considered efficient for other species. Fish were identified in the field using Cadwallader & Backhouse (1983). If identification was uncertain, specimens were preserved in 10% formalin for later examination. The collections of the Museum of Victoria were checked for all fish species with localities in the Otway region.

RESULTS

Eighteen species of freshwater fish, 14 of them native and 4 introduced, have been recorded in the Otway region (Table 1). Species recorded at each site are listed in the Appendix. Species such as the small-mouthed hardyhead (*Atherinosoma microstoma*), Tamar River goby (*Favonigobius tamarensis*) and blue-spot goby (*Pseudogobius olorum*) occur in the estuarine reaches of many of the coastal streams (Cadwallader & Backhouse 1983, Tunbridge & Glenane 1983) but were not encountered during our survey. Similarly, the mainly estuarine flat-headed gudgeon (*Philypnodon grandiceps*) is expected to be more widespread than our results suggest.

The short-finned eel was the most widespread species, occurring at 49 sites. Species of galaxias were also widespread and often abundant, but only one specimen of the Tasmanian mudfish was found (at site 17). Australian grayling were caught at nine sites, but usually as juveniles and usually fewer than 10 in number. Juvenile grayling were captured in the lower reaches of the Cumberland River (Site 14) on 25 February 1987 and whitebait of this species were captured ascending the stream on 24 November 1987. Tupong were generally caught only in the lower reaches of streams. At site 14 tupong were found only below a roadway pipe in which water vel-

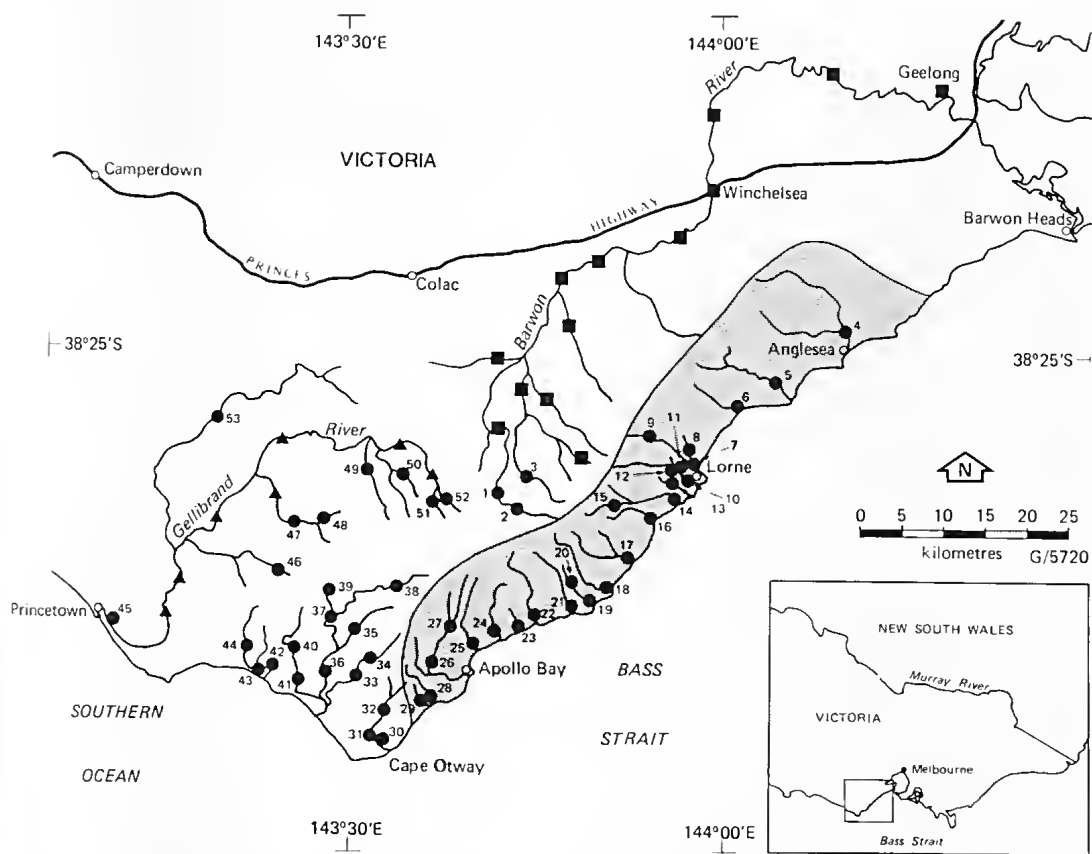


Fig. 1. Sites sampled during our survey (●) and those of Tunbridge & Glenane 1988 (▲) and Hall & Tunbridge 1988 (■). Shaded area indicates region where mountain galaxias, Australian smelt, southern pigmy perch and freshwater blackfish were absent.

oity was high, and at site 7 were not present above steep rapids. Freshwater blackfish were found in some tributaries of the Gellibrand River but not in others having apparently suitable blackfish habitats but subject to extremely heavy sedimentation (sites 49 and 50).

Of the introduced species, only brown trout was widespread throughout the region, being particularly abundant in coastal streams where it was found at 60% of the sites. Only in the Parker River were brown trout absent from all three sites sampled. In the coastal streams only a few specimens of the other three introduced species were caught: mosquitofish at site 12 (St Georges River below the Lorne town water supply storage); two redfin, possibly escaped from the stock in a local dam, at site 6 (Grassy Creek); and one rainbow trout at site 36 in the Aire River.

The native fish fauna of the short coastal

streams differs considerably from that of the Barwon and Gellibrand river systems. Freshwater blackfish, Australian smelt, mountain galaxias and southern pigmy perch were not found in any of the streams between Anglesea and Cape Otway (sites 4 to 29) although these species occurred in streams north of the Otway ridge and west of Cape Otway (Fig. 1). Southern pigmy perch were recorded in the Anglesea river by Atkins & Broune (1982; cited in Raadik 1986) but we could not confirm the occurrence. The mountain galaxias was found in the Parker River (site 32), and freshwater blackfish and Australian smelt were present in the Aire River system. Three large specimens of freshwater blackfish having a maximum size of 527 mm TL were collected at site 36 (Aire River).

This species distribution is consistent with the findings of Renowden (1968) and with the localities of specimens in the Museum of Victoria.

Family	Scientific name	Common name	Abbreviation
Native species			
Mordacidae	<i>Mordacia mordax</i> (Richardson)	Short-headed lamprey	Shlamp
Geotriidae	<i>Geotria australis</i> Gray	Pouched lamprey	Plamp
Anguillidae	<i>Anguilla australis</i>	Short-finned eel	Sfeel
Galaxiidae	<i>Galaxias maculatus</i> (Jenyns)	Common galaxias	Cgal
	<i>Galaxias olidus</i> Gunther	Mountain galaxias	Mgal
	<i>Galaxias brevipinnis</i> Gunther	Broad-finned galaxias	Bgal
	<i>Galaxias truttaceus</i> Valenciennes	Spotted galaxias	Sgal
	<i>Galaxias cleaveri</i> Scott	Tasmanian mudfish	Tmudf
Retropinnidae	<i>Retropinna semoni</i> (Weber)	Australian smelt	Asmelt
Prototroctidae	<i>Prototroctes maraena</i> (Gunther)	Australian grayling	Agrayl
Kuhliidae	<i>Nannoperca australis</i> Gunther	Southern pigmy perch	Sperr
Gadopsidae	<i>Gadopsis marmoratus</i> Richardson	Freshwater blackfish	Fbfish
Bovichthyidae	<i>Pseudaphritis urvillii</i> (Valenciennes)	Tupong	Tup
Eleotridae	<i>Philypnodon grandiceps</i> (Kreffl)	Flat-headed gudgeon	Fhgd
Introduced Species			
Salmonidae	<i>Salmo trutta</i> Linnaeus	Brown trout	Btr
	<i>Oncorhynchus mykiss</i> Walbaum	Rainbow trout	Rtr
Poeciliidae	<i>Gambusia affinis</i> (Baird & Girard)	Mosquitofish	Mosqf
Percidae	<i>Perca fluviatilis</i> Linnaeus	Redfin	Rfin

Table 1. Freshwater fish species found in the Otway region. Abbreviations are those used in Appendix.

DISCUSSION

Geomorphological and climatic influences

During the last glacial epoch (18,000 to 15,000 years BP) the seabed of what is now Bass Strait formed a land link between Tasmania and mainland Australia (Bowler & Hamada 1971). The western edge of the link between King Island and the mainland extended close to the tip of Cape Otway and encompassed the present Otway coastal region (Jennings 1971). The small coastal streams on what is now the eastern side of the Otway Range may not have existed at that time. The rising postglacial sea-level first cut the land link between the Otway region and King Island between 15,000 and 10,000 years BP. The

sea had risen almost to its present level by 5,000 years BP. Since then no major coastal geomorphological changes have occurred (Jennings 1971).

Major climatic changes have also occurred since the glaciation. Sometime after 9,700 years BP the climate around Lake Keilambete, about 70 km northwest of Cape Otway, became wetter, and was wettest between 6,500 years BP and 5,000 years BP (Dodson 1974). The water in the lake later fell to its lowest levels at about 3,500 BP and at about 770 BP; before reaching its highest level in the 19th century (Dodson 1974). The decreases in lake levels may reflect reductions in precipitation or increases in temperature and evaporation (Bowler & Hamada

1971). If the small coastal streams to the east of the Otway Range had been formed by this time they would have been susceptible to droughts and may have flowed intermittently. Interruption to their flow or their complete drying may have destroyed the freshwater fish fauna that had been present in them before about 770 BP.

Evidence that the original fish fauna in these streams may have been destroyed in this way is to be found in the extant native fish fauna consisting entirely of species which have a marine component in their life cycles and which could have recolonised from the sea. In contrast, the Aire, Gellibrand and Barwon river systems contain four species of native fish which spend their entire lives in fresh water. These river systems may not have been effected by the land bridge or, being much larger, were less influenced by the arid conditions.

The Australian smelt, a small forage species, was absent from the coastal streams but has been found in the Aire, Barwon and Gellibrand Rivers (Hall & Tunbridge 1988, Tunbridge & Glenane 1988). Freshwater blackfish are usually more abundant in habitats with low water velocities and with logs and wood debris which are used for instream cover and for spawning sites (Jackson 1978a, 1978b, Koehn 1986d). The coastal streams from which this species was absent are essentially low order streams that are fast-flowing but which commonly contain many pools where water velocity is low and wood debris present. The freshwater blackfish has been recorded in the Aire River system and is widespread throughout the Gellibrand and Barwon Rivers in similar habitats (Hall & Tunbridge 1988, Tunbridge & Glenane 1988). The southern pigmy perch is commonly associated with aquatic vegetation (Cadwallader 1979), with mud substrates (Jackson & Davies 1983), and with slow-flowing or still waters (Llewellyn 1974). Small areas of such habitats are present though not common in the Otway coastal streams, but southern pigmy perch were absent. The species has been recorded from the Gellibrand and Barwon River systems (Hall & Tunbridge 1988, Tunbridge & Glenane 1988).

Mountain galaxias were also absent from the coastal streams but were collected from tributaries of the Gellibrand and Barwon Rivers in habitats similar to those found in the Otway coastal streams. The absence of the mountain galaxias from the coastal streams cannot be attributed to the presence of large numbers of brown trout, which are known to exclude mountain galaxias

(Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Davies 1983), because the latter were collected from tributaries of the Gellibrand and Barwon Rivers where trout were widespread.

The presence of mountain galaxias in the Parker River and of freshwater blackfish, mountain galaxias and Australian smelt in the Aire River system delineates the boundary where fish distribution changes (Fig. 1). Although it is similar in size to other Otway coastal streams, the Parker River in the middle of Cape Otway may not have been subjected to the same geomorphological conditions as streams farther to the east.

The fish fauna in the Otway coastal streams is similar to that in the short coastal streams flowing east from the Mornington Peninsular ridge (Koehn 1986b), which may have been subjected to similar geomorphological and climatic conditions as the Otway region.

There are marked similarities between the native freshwater fish fauna of the Otway region and Tasmania, most species being common to these areas. The distribution of species whose life cycle is spent entirely in freshwater is especially interesting. In Tasmania, the southern pigmy perch, *Nannoperca australis*, and freshwater blackfish, *Gadopsis marmoratus*, occur naturally only in northern rivers flowing into Bass Strait (Frankenberg 1974). The Gadopsidae appears to be an entirely freshwater family that is restricted by salt-barriers. It has been suggested that the severe reduction or obliteration of freshwater streams on the Bass Strait islands during glaciation may have resulted in the extinction of *Gadopsis* from this region (Sanger 1986).

The dwarf galaxias, *Galaxiella pusilla*, was not found in our study area but it is present in western Victoria (Tunbridge & Glenane 1983). Populations of this species are also found on the north coast of Tasmania and on Flinders Island (Frankenberg 1974).

Frankenberg (1974) suggested that the freshwater blackfish, southern pigmy perch and dwarf galaxias migrated to Tasmania from the mainland when the landbridge existed and when continuities of fresh water were likely. In contrast, Sanger (1986), on the basis of work by Watson & Littlejohn (1985), favoured a northward dispersal of the freshwater blackfish from Tasmania. Frankenberg (1974) also suggested that the spotted and broad-finned galaxias may have migrated to the mainland from Tasmania during the same period. However, the occurrence of larval galaxiids as much as 700 km

offshore from New Zealand supports the theory of McDowall (1978) that long-range dispersal of diadromous species may occur despite oceanic barriers.

Recent influences

The distribution of fish species recorded during surveys in other waterways has often been correlated with the availability of suitable habitats (e.g. Cadwallader 1979, Jackson & Davies 1983, Koehn 1986a, 1986b, 1986c) and with access to those habitats. The wide distribution of the short-finned eel in the Otway region is indicative of the wide range of habitats which the species can tolerate (Cadwallader & Backhouse 1983) and of its ability to negotiate barriers. The common galaxias, though less able to negotiate barriers, is also widespread and was found in a variety of habitats. Species with more specific habitat requirements such as freshwater blackfish and tupong, both of which prefer slower-flowing waters (Koehn 1986d, unpublished data), had more restricted distributions. Tupong appear to be particularly susceptible to stream barriers and were not found in the upper reaches of steep streams, although they are found well inland in larger rivers such as the Gellibrand (Tunbridge & Glenane 1983). During our survey tupong were not found above the "rapids" on the Erskine River nor above a road crossing on the Cumberland River consisting of pipes where uniform water velocities were particularly fast.

Freshwater blackfish are common in the Gellibrand and Barwon river systems but were not found in Charleys and Lardners Creeks, tributaries of the Gellibrand River, despite the presence of ample suitable habitat. Both these sites had been subjected to extremely heavy sedimentation, probably due to the establishment of surrounding pine plantations, and this may have contributed to the absence of freshwater blackfish. The eggs of freshwater blackfish die if they remain covered with silt (Koehn unpublished data). Moreover, because this species requires a clean surface on which to lay its adhesive eggs, spawning may not take place or may be unsuccessful if suitable sites are covered by a thick layer of sediment.

Fish distributions in the Otway region probably have not changed markedly in recent years as our results concur with those of Renowden (1968) and Baxter (1985), but a major change has occurred during the past century with the introduction of trout. Brown trout were par-

ticularly abundant in the cool, well-oxygenated waters of the Otway coastal streams, which suit the habit of this species and contain gravel substrates which it requires for spawning (McDowall & Tilzey 1980). Apart from creating widespread populations of a new species, such introductions are likely to have affected the distribution of native fish species.

Published literature suggests that the broad-finned galaxias is usually found in fast-flowing water in the upper reaches of steep, rocky streams (Cadwallader & Backhouse 1983). Our results show that the species is also found in slow-flowing reaches of streams where the short-finned eel was the only other species present. The distribution of the broad-finned galaxias may be severely affected by the presence of other species, particularly brown trout (Jackson & Williams 1980) which at some sites appeared to restrict the broad-finned galaxias to shallow riffles not accessible to trout (Koehn unpublished data). Brown trout are voracious predators and in many areas fish can form a large part of their diet. The effects of brown trout on the distribution of the mountain galaxias are more comprehensively documented, mutually exclusive populations of these two species being common (Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Davies 1983). It has been suggested that brown trout may also be detrimental to Australian grayling, *Prototroctes maraena* (Jackson & Koehn 1988).

The other three introduced species in the Otway coastal streams were neither abundant nor widespread, in contrast to the large numbers of six introduced species present in the Barwon and Gellibrand Rivers (Cadwallader & Backhouse 1983, Hall & Tunbridge 1988, Tunbridge & Glenane 1988). Predation, particularly by trout and redfin, as well as competition for food and space by introduced species can be especially detrimental to native fish populations (Cadwallader & Backhouse 1983). The introduction of additional exotic species should therefore be avoided.

CONSERVATION AND MANAGEMENT

The Otway region, in particular the Otway Range, is considered to be an important conservation area where many streams have been given high conservation status (Tunbridge & Glenane 1983, Macmillan et al. 1987). Although none of the fish species found in the region is considered endangered at present, several species are con-

sidered to be under some threat (Cadwallader et al. 1984).

The fish species with the greatest conservation need in the Otway region is the Australian grayling. This species was classified by Cadwallader et al. (1984) as "vulnerable in Victoria" but is likely to be considered endangered in the near future if the population continues to decline. Australian grayling were collected from nine sites in the study area, most of the samples consisting of a few young individuals taken from coastal streams. More than 100 Australian grayling have been taken from a population monitored in the Barwon River (Hall & Tunbridge 1988, Jackson & Koehn 1988). The collection of Australian grayling whitebait ascending the Cumberland River adds to our knowledge of the lifecycle of this species. The Otway region should be considered an important conservation area for this species because of its widespread distribution in coastal streams.

The broad-finned galaxias, the spotted galaxias and the Tasmanian mudfish were all listed by Cadwallader et al. (1984) in Category C; that is, species that are rare or have a restricted distribution in Victoria. Broad-finned and spotted galaxias were widespread and abundant in the Otway coastal streams. The Tasmanian mudfish was first found on mainland Australia at Wilsons Promontory (Jackson & Davies 1982). Discovery of a specimen in Wye River in 1983 extends the known range of the species into western Victoria. The swamp areas normally inhabited by adults of this species pose sampling difficulties, and a study of the whitebait stage (Fulton 1986) may determine other localities.

The conservation status in Victoria of the pouched lamprey, which was recorded at six sites, has been listed as "indeterminate", i.e. possibly threatened (Category D of Cadwallader et al. 1984).

Because the fish fauna of the Otway coastal streams consists of species which need to migrate between the sea and fresh water at some stage of their lifecycles, the maintenance of fish passage in these streams is important. Passage of many species into the upper reaches of several streams is restricted by natural barriers such as waterfalls. Only short-finned eels and broad-finned galaxias occur naturally above such barriers, an indication of the extraordinary climbing and migratory capabilities of these species. Most other species are much more restricted by stream barriers and are thus more easily cut off from available habitat by small weirs or culverts.

The native freshwater species most widely sought by anglers in southern Victoria is the freshwater blackfish (Barnham 1983). One of Victoria's most valuable populations of this species is found in the Gellibrand River which has the highest reported percentage of freshwater blackfish longer than the minimum legal length (220 mm TL). This river is one of the few that still contain large specimens of this species (Tunbridge & Glenane 1988).

Not surprisingly, the Gellibrand River is one of the most popular freshwater fishing venues in Victoria. Most anglers (76%) on the Gellibrand River seek freshwater blackfish (Koehn 1984) and are attracted by the prospect of catching a trophy fish. The range of this species has been considerably reduced (Jackson & Llewellyn 1980) and the Gellibrand River needs to be given a high level of protection. Careful land management and the provision of adequate buffer strips are required to avoid the heavy sedimentation seen at two sites.

The Gellibrand and Barwon Rivers are classified as sport fisheries for the freshwater blackfish (Tunbridge & Glenane 1983), and streams in the Otway region provide many opportunities for anglers seeking brown trout. Large numbers of brown trout of suitable size were present at most of the sites we sampled and, despite decreases in stockings, most streams have viable, self-maintaining populations of this species.

The Otway region contains a valuable assemblage of mainly native freshwater fish and the introduction of other species should be prevented. The region provides excellent conservation areas for many fish species in addition to opportunities for recreational angling for freshwater blackfish and brown trout. Most of the streams maintain riparian vegetation, instream cover and substrate free of silt, all attributes which have been lost from many river systems. If these valuable fish faunas and their habitats are to be retained, careful management is needed.

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APPENDIX

Localities sampled and species present.

Site No.	Stream Name	Map No.	Grid Ref.	Date Sampled	Species Present
1	West Barwon Dam	7620	360 290	29.7.88	Sfecl, Cgal, Btr
2	West Barwon R	7620	370 264	19.1.88	Sfecl, Cgal, Fbfish, Btr
3	East Barwon R	7620	393 294	21.1.88	Sfecl, Mgal, Fbfish, Btr
4	Anglesea R	7721	540 463	1977, 1981	Sfecl, Cgal, Sgal
5	Painkalac Ck	7721	460 403	24.3.87	Plamp, Sfecl, Cgal, Sgal
6	Grassy Ck	7721	407 362	24.2.87	Sfecl, Cgal, Sgal, Bgal, Agrayl,
				6.5.87	Tup, Fhgud, Btr, Rfin
7	Erskine R	7620	590 305	4.3.86	Plamp, Sfecl, Cgal, Bgal,
				March 1987	Sgal, Agrayl, Tup, Fhgud, Btr
8	Little Erskine R	7620	588 312	5.3.86	Sfecl, Cgal, Bgal
9	Erskine R	7620	538 337	March 1987	Sfecl, Btr
10	St Georges R	7620	577 288	25.2.87	Sfecl, Cgal, Sgal, Btr
11	Cora Lynne Ck	7620	571 303	17.3.87	Plamp, Sfecl, Bgal, Btr
12	St Georges R	7620	565 300	25.2.87	Sfecl, Bgal, Mosqf
13	She-Oak R	7620	563 284	24.2.87	Sfecl, Bgal, Btr
14	Cumberland R	7620	566 264	25.2.87	Plamp, Sfecl, Cgal, Sgal, Bgal, Agrayl, Tup, Btr
15	Cumberland R	7620	260 487	2.3.87	Sfecl, Bgal
16	Jamieson R	7620	540 238	17.7.87	Sfecl, Cgal, Bgal, Sgal
17	Wye R	7620	514 196	14.9.83	Lamp, Cgal, Sgal, Tmudf,
				30.4.84	Agrayl, Tup, Btr
				14.11.84	
18	Kennett R	7620	487 162	26.2.87	Sfecl, Cgal, Bgal, Sgal, Agrayl, Fhgud, Tup, Btr
19	Grey R	7620	468 145	2.5.84	Sfecl, Cgal, Sgal, Btr
20	Grey R	7620	450 171	1974	Sfecl, Bgal
21	Carisbrook Ck	7620	443 135	15.11.84	Sfecl, Cgal, Sgal, Agrayl, Btr
22	Smythes Ck	7620	400 124	26.2.87	Sfecl, Cgal, Bgal, Sgal, Btr
23	Browns Ck	7620	380 113	21.5.87	Sfecl, Cgal, Sgal, Btr
24	Skenes Ck	7620	350 106	26.2.87	Sfecl, Cgal, Sgal, Agrayl, Tup, Btr
25	Wild Dog Ck	7620	327 097	12.1.84	Plamp, Sfecl, Cgal, Bgal, Sgal,
				8-10.5.84	Agrayl, Tup, Fhgud, Btr
26	Barham R	7620	280 072	1.3.82	Sfecl, Cgal, Sgal, Agrayl,
				19.5.83	Tup, Btr
27	Barham R	7620	291 016	18.5.83	Sfecl, Cgal, Btr
28	Elliott R	7620	272 039	1974	Sfecl, Bgal
29	Geary R	7620	264 033	1974	Bgal
30	Parker R	7620	205 975	18.11.88	Sfecl, Cgal, Bgal, Sgal
31	Parker R	7620	205 975	3.3.87	Sfecl, Bgal
32	Parker R	7620	218 025	3.3.87	Sfecl, Mgal, Bgal
				19.1.88	
33	Calder R	7620	180 054	3.3.87	Sfecl, Cgal, Sgal, Fbfish, Btr
34	Calder R	7620	187 075	3.3.87	Sfecl, Bgal, Btr
35	Clearwater Ck	7620	184 103	3.3.87	Sfecl, Mgal, Bgal

36	Aire R	7520	148 072	27.11.86 6.8.87 15.2.88 20.1.88	Shlamp,Sfeel,Cgal, Sgal,Asmelt,Agrayl, Fbfish,Tup,Fhgud, Btr,Rtr
37	Aire R	7520	152 131	9.12.86	Sfeel,Bgal,Btr
38	Aire R	7620	232 165	9.12.86	Sfeel,Bgal,Btr
39	Young Ck	7520	168 168	5.3.87	Bgal,Btr
40	Ford R	7520	105 099	5.3.87	Plamp,Sfeel,Sgal,Fbfish,Btr
41	Ford R	7520	112 052	5.3.87	Shlamp,Plamp,Sfeel,Cgal,Sgal,Btr
42	Johanna R (east)	7520	080 077	16.7.87	Lamp,Sfeel,Cgal,Bgal,Sgal
43	Johanna R	7520	063 072	16.7.87	Plamp,Sfeel,Cgal,Btr
44	Johanna R	7520	055 094	16.7.87	Sfeel,Bgal
45	Gellibrand R	7520	892 144	24.11.87	Cgal
46	Chapple Ck	7520	040 193	21.1.88	Sfeel,Bgal,Fbfish,Btr
47	Carlisle R	7520	107 245	21.1.88	Sfeel,Sgal,Fbfish,Btr
48	Carlisle R	7520	168 255	21.1.88	Plamp,Sfeel,Btr
49	Charleys Ck	7620	210 287	21.1.88	Sfeel,Sgal,Btr
50	Lardners Ck	7620	238 295	20.1.88	Lamp,Sfeel,Btr
51	Asplin Ck	7620	287 273	20.1.88	Mgal
52	Gellibrand R	7620	313 268	20.1.88	Shlamp,Sfeel,Bgal,Btr
53	Tomahawk Ck	7521	020 368	4.3.87	Sfeel,Cgal,Spper

Lamprey ammocoetes observed but not captured at sites 17, 42 and 50 could not be identified to species level but are recorded as Lamp.

A FLORISTIC SURVEY OF THE DERRIMUT GRASSLAND RESERVE, MELBOURNE, VICTORIA

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LUNT, I. D., 1990:05:31. A floristic survey of the Derrimut Grassland Reserve, Melbourne, Victoria. *Proceedings of the Royal Society of Victoria* 102(1): 41–52. ISSN 0035-9211.

The 154 ha Derrimut Grassland Reserve contains the largest *Themeda* grassland on public land on the basalt plains of western Victoria. It includes three types of wetland and two of grassland. Wetland vegetations appear to be dependent upon the duration of seasonal flooding, and grassland vegetations on previous land use, particularly ploughing. A total of 102 species of native plants and 78 exotics are listed; three native species are rare or vulnerable in Victoria.

ONE of the most important issues for nature conservation in temperate Australia is the preservation of native grasslands and grassy woodlands. Grasslands of *Themeda*, *Stipa*, *Danthonia* and *Poa* once dominated extensive areas of temperate New South Wales, Victoria, Tasmania and south-eastern South Australia but were rapidly destroyed by agriculture. Today only small patches remain, few of them protected in conservation reserves (Groves 1979, Specht 1981a, Davies 1982, Frood & Calder 1987, Kirkpatrick et al. 1988).

The original *Themeda* grasslands were dominated by *T. triandra* with sub-dominant *Danthonia* and *Stipa* species. The grasses formed discrete tussocks rather than a closed turf, and a variety of herbs, particularly composites, grew on the bare earth in the inter-tussock spaces (Patton 1935, Willis 1964).

Many of the most diverse remnants of *Themeda* grassland in Victoria are on railway reserves that have been burnt regularly and grazed infrequently over the past 100 years (Stuwe & Parsons 1977, Stuwe 1986). If grasslands are to be effectively protected, then the narrow and typically small remnants of railway reserves must be supplemented by larger remnants; invariably these have been grazed and are of lower diversity than rail-line remnants (Stuwe & Parsons 1977).

The Keilor basalt plains, immediately west of Melbourne, encompass many of the best, large remnants of *Themeda* grassland in western Victoria (Stuwe 1986) plus two of the largest reserves for *Themeda* grassland in the State: the Laverton North and Derrimut Grassland Re-

serves, of 40 ha and 154 ha respectively. This paper presents the results of a floristic survey of the Derrimut Grassland Reserve.

SITE DESCRIPTION

The Derrimut Grassland Reserve occupies 154 ha on the north-eastern corner of Boundary and Fitzgerald Roads in the City of Sunshine, 14 km west of Melbourne. The mean annual rainfall at Laverton, 7 km SSW of the reserve, is 568 mm (Bureau of Meteorology, unpublished data) and is evenly distributed throughout the year. The maximum monthly mean temperature is 26°C in January and the mean minimum is 5°C in July. The reserve is situated on the Keilor basalt plains, the underlying rock being olivine basalt belonging to the Newer Volcanics, of Early Pleistocene age (Mines Department, undated; Douglas 1982). Surface rock is locally abundant in the reserve and the topography is gently undulating (Fig. 1). Most soils are duplex but gradational soils occur in some areas of low elevation and poor drainage. Topsoils are of silty clay, silty clay loam and clay loam, and generally are neutral to slightly basic, with pH ranging from 6.0 to 7.5. Hummocks about 1 m in diameter and depressions ("gilgai" topography) in the north-east of the reserve reflect small-scale variations in the soil profile (Lunt 1987). A semi-permanent lake called Lake Stanley or Andersons Marsh occupies an area of about 15 ha in the southern part of the reserve (Fig. 1). A major drainage line flows intermittently into Lake Stanley from the north-west, and a minor drainage line flows from the north-east.

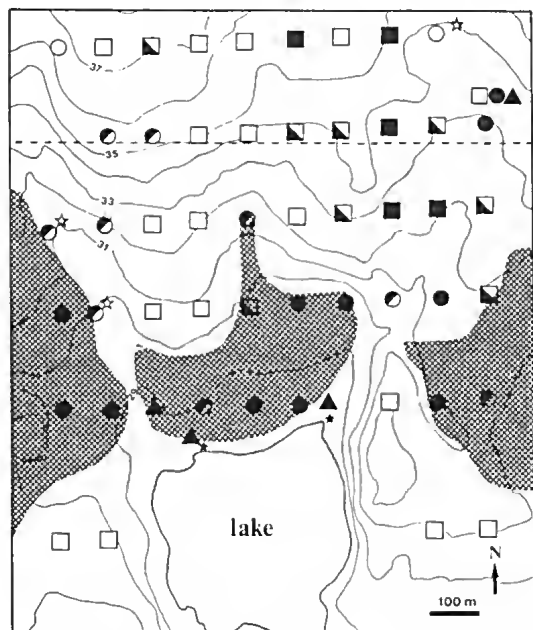


Fig. 1. Distribution of vegetation types in 61 quadrats in Derrimut Grassland Reserve. Open, semi-closed and closed circles and squares denote species-poor, moderate and species-rich *Vulpia* grassland and *Themeda* grassland respectively; open stars denote *Eleocharis* sedgeland; closed stars denote *Amphibromus-Agrostis* grassland; triangles denote mixed-species hermland. Shaded areas were ploughed last century. Contour interval is 1 m (Melbourne & Metropolitan Board of Works 1978). Horizontal dotted line denotes an old fence.

SITE HISTORY

The property was owned by the Myers family from 1912 until the 1950s when it was bought by the Victorian Government, but it was grazed by the family's stock until 1985 (D. Myers, personal communication; source also of the following agricultural information). Three to four hundred head of sheep (3 to 4 per hectare) were run until the late 1960s when they were replaced by 80 to 90 head of cattle. On two occasions in the early 1960s the site was heavily grazed for a fortnight by 6,000 to 7,000 sheep. Although all of the vegetation was consumed, *Themeda triandra* and other grasses recovered after the first rains. The property was divided in two by an east-west fence (Fig. 1). Grazing pressure was greater in the southern paddock and where cattle congregated at the western end of the fence. Three areas of the reserve were ploughed, and presumably

cropped, in the late 1800s (Fig. 1) but there has been no ploughing or cropping since 1912 and probably none since 1900. The site was rarely burnt and superphosphate was never applied.

METHODS

Sampling

Minimal quadrat area (defined as the point at which a 10% increase in area yields only a 5% increase in species; Mueller-Dombois & Ellenberg 1974) was determined from two sites dominated by *T. triandra*, and was found to be between 9 m² and 11 m². A quadrat size of 15 m² (5 × 3 m) was employed.

Quadrats were sampled in November and December of 1986 and 1987. Fifty-one were located at 100 m intervals on six transects set 200 m apart and ten were selectively placed in vegetations that were inadequately sampled on transects (Fig. 1). Quadrats were orientated to include uniform vegetation. In each quadrat, the cover of all species of vascular plants was recorded using the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974), with the Braun-Blanquet category "r" being included in the category "+". The reserve was exhaustively traversed between November 1986 and January 1988 and a comprehensive list made of all species not found in quadrats. Plant taxonomy follows Forbes & Ross (1988), and exotic species are marked with an asterisk. Specimens of many species are lodged with the National Herbarium of Victoria (MEL).

Classification

The program MAGIC — a polythetic, agglomerative, non-hierarchical cluster analysis utilizing presence/absence data (Gullan 1978) — was used to classify quadrats according to floristic composition. Quadrat and species groups from the classification were hand-sorted for clearer resolution of the floristic table. Data are permanently stored on the database of the Flora and Fauna Survey Group of the Department of Conservation, Forests and Lands of Victoria, as quadrats B18181 to B18234 (quadrats 1 to 54) and E01401 to E01407 (quadrats 55 to 61).

The Tukey-Kramer test, suitable for unplanned, multiple comparisons among pairs of means based on unequal sample sizes (Sokal & Rohlf 1981), was used to test differences in species-richness between vegetation groups.

RESULTS AND DISCUSSION

Plant species

One hundred and eighty species of vascular plants were recorded from the reserve (see Appendix), including 102 natives (57% of species) and 78 exotics (43%). All but six species were herbs and many of the most widespread species in the reserve were exotic (Table 1). Three of the native species recorded are rare or vulnerable in Victoria: *Comesperma polygaloides*, *Stipa gibbosa* and *Stipa setacea* (Gullan et al., in prep.). The reserve included 26% of the 391 species of native plants that occur on the Keilor basalt plains (Willis 1964). Although Asteraceae, Poaceae and Cyperaceae were the largest families in the reserve and on the plains in general, many large families on the plains were absent from or poorly represented at Derrimut; for example, the reserve included only one of 15 orchid species, two of 13 native legumes and none of the 14 native chenopods recorded from the Keilor basalt plains.

Vegetation types

Two major vegetation groups, wetland vegetation and grassland vegetation, were identified from the floristic table (Table 2). They were divided into five minor groups, comprising three wetland vegetations (*Amphibromus-Agrostis* grassland, *Eleocharis* sedgeland and mixed-species herbland) and two grassland vegetations (*Themeda* grassland and *Vulpia* grassland).

The five minor groups were differentiated by floristic and structural features, and their names refer to the dominant species and vegetation

structure (after Specht 1981b): mixed-species herbland was co-dominated by a number of species. In the following discussion, "grasslands" refer to *Themeda* and *Vulpia* grasslands and do not include the minor wetland group, *Amphibromus-Agrostis* grassland, unless otherwise noted. The term "species richness" denotes the mean number of species in each quadrat.

Wetland vegetation

"Wetland vegetation" is a convenient name to encompass three minor groups of diverse structure and composition but similar habitat. They occurred in areas that were seasonally or almost permanently inundated: the margins of Lake Stanley and small depressions along drainage lines and within grasslands. The eastern drainage line did not carry surface water for sufficiently long periods to support wetland vegetation.

Amphibromus-Agrostis grassland was co-dominated by *Amphibromus nervosus* and *Agrostis avenacea* (Fig. 2). It was restricted to a narrow band on the edge of Lake Stanley (Fig. 1) which was inundated for almost the entire period of observation (November 1986 to January 1988). Species richness was very low: on average, only 12 species occurred per quadrat (Fig. 3).

Eleocharis sedgeland, dominated by *Eleocharis acuta*, occurred in small depressions throughout the reserve (Figs 1, 4) and was most common in the numerous depressions along the western drainage line. It was inundated seasonally, but surface water evaporated in summer causing the silty clay soils to crack deeply. Species richness was very low: viz. 11 species per quadrat (Fig. 3). *Eleocharis* sedgeland was floristically related to *Amphibromus-Agrostis* grass-

Species	%	Species	%
* <i>Romulea rosea</i>	92	* <i>Leontodon taraxacoides</i>	39
* <i>Vulpia bromoides</i>	92	<i>Schoenus apogon</i>	39
* <i>Lolium rigidum</i>	74	<i>Eryngium ovium</i>	38
<i>Themeda triandra</i>	74	<i>Juncus bufonius</i>	38
<i>Convolvulus erubescens</i>	67	* <i>Plantago coronopus</i>	38
* <i>Briza minor</i>	66	<i>Acaena echinata</i>	36
* <i>Bromus hordeaceus</i>	59	<i>Danthonia setacea</i>	36
<i>Oxalis perennans</i>	59	* <i>Briza maxima</i>	34
* <i>Aira cupaniana</i>	56	* <i>Cyperus tenuis</i>	34
<i>Stipa bigeniculata</i>	56	* <i>Cicendia quadrangularis</i>	33
<i>Danthonia duttoniana</i>	41	* <i>Trifolium striatum</i>	33
* <i>Hypochaeris radicata</i>	41	* <i>Trifolium subterraneum</i>	33

Table 1. Species recorded from 33% or more of quadrats and percentage of quadrats in which each occurred. Asterisks show exotic species.



Fig. 2. *Amphibromus-Agrostis* grassland on edge of Lake Stanley, December 1986; tape measure encloses a 5 × 3 m quadrat.

land (Table 2). Its recognition as a separate group was based on differences in habitat, dominance and appearance as well as floristics.

Mixed-species herbland was co-dominated by a variety of herbs, each of which generally occurred at low cover values. Common species included *Eleocharis acuta* (to 150 mm tall only), *Lobelia pratensis*, *Danthonia duttoniana*, *Agrostis avenacea* and **Leontodon taraxacoides* (Fig. 5). This vegetation type was most extensive in a broad zone around Lake Stanley, behind the narrow band of *Amphibromus-Agrostis* grassland, but it also occurred in places along the drainage lines (Fig. 1). It was seasonally flooded but for a shorter period than *Amphibromus-Agrostis* grassland or *Eleocharis* sedgeland. Bare soil was often abundant and deep cracks appeared in late summer. In contrast to the other wetland groups, species richness was very high:

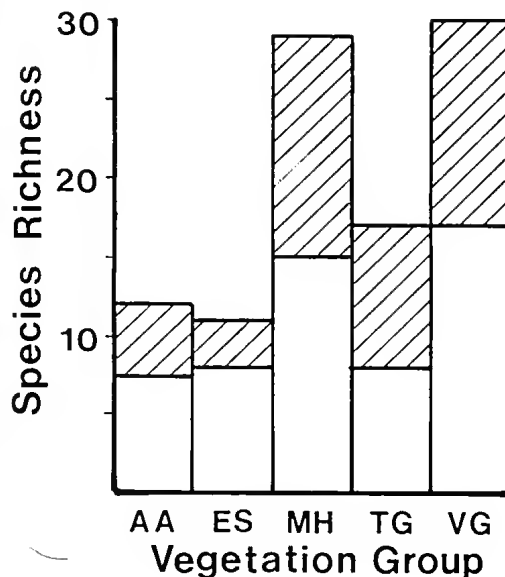


Fig. 3. Mean number of total, native and exotic species in five vegetation types; hatching shows exotic species. AA = *Amphibromus-Agrostis* grassland, ES = *Eleocharis* sedgeland, MH = mixed-species herbland, TG = *Themeda* grassland, VG = *Vulpia* grassland.

viz. 29 species per quadrat (Fig. 3). However, the mean number of exotics per quadrat (15 species) was greater than in all other vegetations (Fig. 3). The total number of species in mixed-species herbland was significantly greater than in *Themeda* grassland and *Eleocharis* sedgeland, and the number of exotic species was significantly greater than in *Themeda* grassland, *Eleocharis* sedgeland and *Amphibromus-Agrostis* grassland ($p \leq 0.05$).



Fig. 4. *Eleocharis* sedgeland in small depression on western drainage line, December 1986; *Potamogeton tricarlinatus*, **Lilaea scilloides* and *Myriophyllum* sp. dominate central depression.



Fig. 5. Mixed-species herbland, December 1986; species include *Eryngium vesiculosum*, *Lobelia pratensis* and *Danthonia duttoniana*.

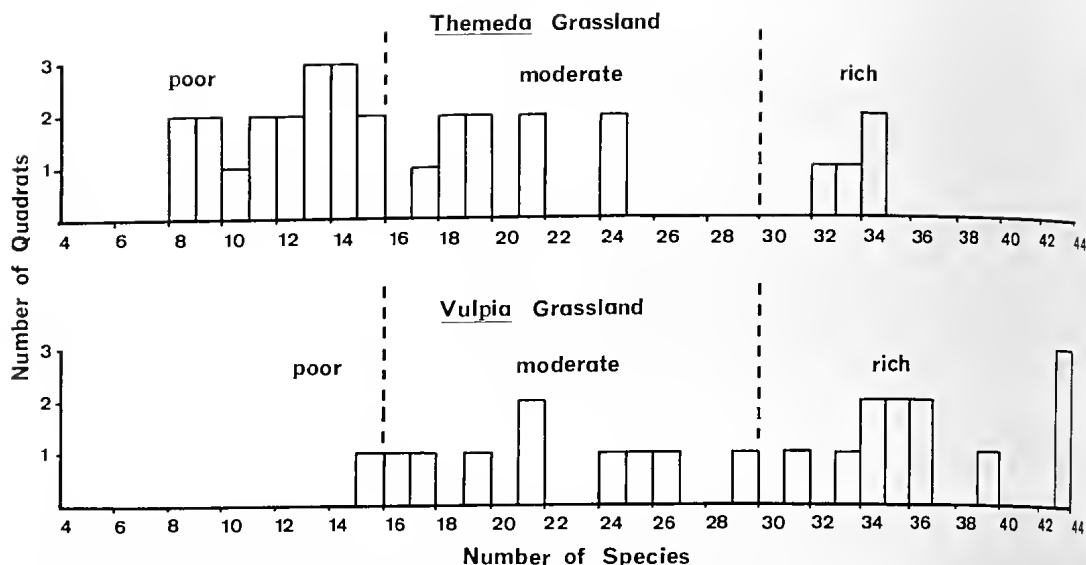


Fig. 6. Number of species recorded from quadrats in *Themeda* and *Vulpia* grassland, and boundaries drawn between species-poor, moderate and species-rich grassland.

Grassland vegetation

The minor grassland groups were differentiated by dominance rather than by floristics, as discrete floristic groups are not easily recognised from Table 2. Instead, it shows a gradual transition from species-rich to species-poor quadrats, regardless of dominant species. Quadrats in which *T. triandra* cover was greater than 25% (i.e. Braun-Blanquet cover values 3 to 5) were defined as *Themeda* grassland; in all but four of such cases *T. triandra* cover exceeded 50% (i.e. obtained a cover value of 4 or 5). Quadrats in which *T. triandra* cover was less than 25% were defined as *Vulpia* grassland; *T. triandra* cover exceeded 5% (i.e. obtained a cover value of 2 to 5) in only three such cases. Despite this arbitrary distinction, the two groups were generally easily recognisable in the field. *Themeda* and *Vulpia* grasslands were divided into three sub-units — species-poor, moderate and species-rich — in order to illustrate general patterns of species-richness in the reserve (Fig. 1). The boundaries between the sub-units were based on arbitrary discontinuities in species richness between quadrats (Fig. 6), and are indicated on the floristic table (Table 2) by dotted horizontal lines.

Themeda grassland was the most widespread vegetation in the reserve (Fig. 1), and occurred in well-drained areas which were not ploughed last century and which were heavily grazed only briefly this century (see site history). In most

areas *T. triandra* exceeded 90% cover (Fig. 7). On average, 17 species occurred in each quadrat, including nine exotics and eight natives (Fig. 3), but most quadrats possessed few individuals of few species. Discrete, species-rich patches occurred amongst areas that were generally species-poor. The patches were visually distinctive as tussocks of *T. triandra* were short and stunted and flowering culms were less abundant than in species-poor grassland. Native herbs such as *Helichrysum apiculatum* and *Leptorhynchus squamatus* were usually abundant. The patches were not associated with variations in physical soil features, such as soil texture, colour or pH.



Fig. 7. Species-poor *Themeda* grassland with almost complete cover of *T. triandra*, December 1986; tape measure encloses a 5 × 3 m quadrat.

but may reflect low levels of soil moisture from late spring to early autumn (Lunt 1987); insufficient soil moisture may possibly restrict the growth of *T. triandra* and prevent it from out-competing herbs.

Vulpia grassland was dominated by the exotic annual **Vulpia bromoides*, often with sub-dominant *Stipa bigeniculata* and occasionally with the exotic **Stipa neesiana* (Fig. 8). This grassland occurred along drainage lines and in areas that were ploughed last century or grazed heavily this century, such as the western end of the fence that once divided the reserve (Fig. 1). The cover of *T. triandra* in *Vulpia* grassland was slightly under-estimated as quadrats were orientated to include uniform vegetation, and consequently to avoid small patches of *T. triandra*. With the possible exception of some sites along the drainage lines, areas of *Vulpia* grassland

were probably dominated by *T. triandra* prior to ploughing and grazing. The abundance in *Vulpia* grassland of exotics such as **Briza minor*, **Lolium rigidum*, **Trifolium* species and **Romulea rosea* probably reflected the relatively open cover. Most of these species were common in *Themeda* grassland as soil-stored seed (Lunt 1990a) but germination was presumably suppressed by the closed sward. These species regenerated profusely when the *Themeda* grassland was burnt (Lunt 1990b). *Vulpia* grassland contained significantly more native species than *Themeda* grassland, and significantly more exotics than *Themeda* grassland, *Amphibromus-Agrostis* grassland and *Eleocharis* sedgeland ($p < 0.05$). Areas ploughed last century were amongst the most diverse in the reserve. On average, 17 natives and 13 exotics occurred in each quadrat (Fig. 3).



Fig. 8. Species-rich *Vulpia* grassland with forbs including *Convolvulus erubescens*, *Helichrysum apiculatum* and *Eryngium rostratum*; *Themeda* grassland occurs in background. Photographed in December 1986.

Original vegetation

Due to the almost complete destruction of the native vegetation of the basalt plains and the marked modification of relict patches, especially by the establishment of exotic species, it is almost impossible to reconstruct accurately the vegetation of the Derrimut reserve as it existed at the time of European settlement. However, the following points may be made.

The area was a natural grassland, devoid of trees (Stuwe 1986, McDougall 1987), with *T. triandra* dominating in all well-drained areas. The density of *T. triandra* was probably lower and native herbs were presumably more common in the abundant inter-tussock spaces. Patton (1935) illustrated a quadrat in *Themeda* grassland with 16 native species in 0.8 m², a species richness far greater than that recorded from Derrimut. Many species were presumably depleted or eliminated by continual grazing, a lack of burning and isolation from seed sources in undisturbed grassland remnants. Native orchids, legumes, chenopods and lilies are now particularly rare. Circumstantial evidence of species losses is provided by the ratio of native grasses to native forbs, since grasses are generally more tolerant than forbs of grazing and trampling (Crawley 1983). Whereas grasses comprise only 10% of the native species on the Keilor Plains, and 13% of those in an ungrazed rail reserve at St Albans (Willis 1964, Groves 1965), they comprise 27% of native species in the Derrimut reserve and, similarly, 26% of those in the Laverton North Grassland Reserve (Platt 1983 and unpublished data). This high

proportion of grasses probably reflects the elimination of many native forbs — and possibly, to a minor extent, the ingress of some native grasses — throughout a century of grazing.

Lake Stanley appears to have formed when Boundary Road was constructed on its southern edge. From the topography, it is suspected that the lake site was originally flooded by shallow water for only a short period of the year. Consequently, the present distribution and composition of mixed-species hermland and *Amphibromus-Agrostis* grassland undoubtedly differ from the original. A few shrubs of *Muehlenbeckia cunninghamii* survive on the lake edges, and this species may originally have dominated above a species-rich hermland. Relict swamps dominated by lignum occur elsewhere in the region (McDougall 1987). Changes to the drainage patterns due to road building, to pugging of the soil by stock, and to the replacement of perennial by annual grasses in nearby paddocks, are also likely to have modified the original vegetation of the drainage lines.

Few floristic data are available from comparable vegetations in Victoria. *Themeda* grassland at Derrimut is similar in composition to that described from grazed paddocks and rail easements on the basalt plains of western Victoria (Groves 1965, Stuwe & Parsons 1977, Stuwe 1986), and *Themeda* and *Vulpia* grasslands appear distantly related to the "*Eucalyptus viminalis*/*Eucalyptus ovata*/*Eucalyptus pauciflora*-*Convolvulus erubescens* grassy woodland" community (Evc) in the Midlands of Tasmania (Kirkpatrick et al. 1988). Virtually no floristic data are available from seasonal wetlands on the basalt plains. Wetland vegetations at Derrimut are among the "shallow swamps on basalt" which are in need of "urgent protection" in Victoria (Frood & Calder 1987), and further surveys are urgently required.

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APPENDIX

Vascular plants of the Derrimut Grassland Reserve. Nomenclature follows Forbes and Ross (1988). Asterisks denote exotic species.

PTERIDOPHYTA

ADIANTACEAE

Cheilanthes sieberi

MARSILEACEAE

Marsilea hirsuta

ANGIOSPERMAE

MONOCOTYLEDONEAE

CYPERACEAE

Carex inversa

**Cyperus eragrostis*

**Cyperus tenellus*

Eleocharis acuta

Eleocharis pusilla

Isolepis hookeriana

Isolepis marginata

Schoenus apogon

IRIDACEAE

**Romulea rosea*

JUNCACEAE

Juncus bufonius

**Juncus capitatus*

Juncus flavidus

Juncus holoschoenus

Juncus homalocaulis

Juncus radula

Juncus subsecundus

JUNCAGINACEAE

**Lilaea scilloides*

LILIACEAE

**Allium vineale*

Caesia calliantha

Dianella revoluta

Hypoxis sp.

Tricoryne elatior

Wurmbea dioica

ORCHIDACEAE

Microtis? *unifolia*

POACEAE

Agrostis avenacea

**Aira cupaniana*

Amphibromus nervosus

**Anthoxanthum odoratum*

**Avellinia michelii*

**Avena fatua*

Bothriochloa macra

**Briza maxima*

**Briza minor*

**Bromus hordeaceus*

Chloris truncata

**Critesion hystrix*

**Critesion murinum* ssp. *leporinum*

**Critesion maritimum*

**Cynodon dactylon*

**Dactylis glomerata*

Danthonia auriculata

Danthonia caespitosa

Danthonia carphoides

Danthonia duttoniana

Danthonia eriantha

Danthonia racemosa

Danthonia setacea

**Desmazeria rigida*

Deyeuxia quadriseta

Dichelachne crinita

Elymus scabrus

Eragrostis brownii

**Gastridium phleoides*

**Hainardia cylindrica*

**Holcus lanatus*
**Lolium rigidum*
**Nassella trichotoma*
Panicum effusum
Panicum prolutum
**Paspalum distichum*
Pentapogon quadrifidus
**Phalaris minor*
Poa labillardieri
Poa sieberiana
**Polypogon monspeliensis*
Stipa bigeniculata
Stipa gibbosa
**Stipa neesiana*
Stipa rudis
Stipa setacea
Thiameda triandra
**Tribolium acutiflorum*
**Vulpia bromoides*
**Vulpia myuros forma megalura*

POTAMOGETONACEAE
Potamogeton tricarlinatus

DICOTYLEDONEAE

AMARANTHACEAE
Ptilotus macrocephalus
Ptilotus spathulatus

APIACEAE
Eryngium ovinum
Eryngium vesiculosum

ASTERACEAE
**Arctotheca calendula*
Brachyscome basaltica
Brachyscome heterodonta
Calocephalus citreus
Calotis anthemoides
Calotis scapigera
Centipeda cunninghamii
**Cirsium vulgare*
**Cotula coronopifolia*
Craspedia chrysantha
Craspedia glauca
**Cynara cardunculus*
Gnaphalium indutum
Gnaphalium polycaulon
**Gnaphalium purpureum*
**Hedypnois cretica*
Helichrysum apiculatum
Helichrysum rutidolepis
**Hypochoeris glabra*
**Hypochoeris radicata*
**Leontodon taraxacoides*
Leptorhynchus squamatus
*Microseris scapigera*¹
Minuria leptophylla

Myriocephalus rhizocephalus
**Picris echioides*
Podolepis jaceoides
**Scorzonera laciniata*
Senecio quadridentatus
Solenogyne dominii
**Sonchus asper*
**Sonchus oleraceus*
**Tragopogon porrifolius*
Vittadinia cuneata

BRASSICACEAE

**Lepidium* sp.

CAMPANULACEAE

Lobelia pratensis
Wahlenbergia communis
Wahlenbergia gracilentia

CARYOPHYLLACEAE

**Cerastium glomeratum*
**Sagina procumbens*
Spergularia rubra
Stellaria palustris

CLUSIACEAE

Hypericum gramineum
**Hypericum perforatum*

CONVOLVULACEAE

**Convolvulus arvensis*
Convolvulus erubescens
Dichondra repens

CRASSULACEAE

Crassula decumbens

CUSCUTACEAE

**Cuscuta epithymum*

DROSERACEAE

Drosera peltata ssp. *peltata*

FABACEAE

Desmodium varians
Glycine tabacina
**Medicago polymorpha*
**Trifolium angustifolium*
**Trifolium campestre*
**Trifolium dubium*
**Trifolium glomeratum*
**Trifolium repens*
**Trifolium striatum*
**Trifolium subterraneum*
**Vicia* sp.

GENTIANACEAE

**Centaurium tenuiflorum*

¹ *Microseris scapigera*
 recorded by N. H. Scarlett (pers. comm.)

**Cicendia filiformis*
 **Cicendia quadrangularis*
Sebaea ovata

GERANIACEAE

**Erodium botrys*
 **Geranium dissectum*

GOODENIACEAE

Goodenia gracilis
Velleia paradoxa

HALORAGACEAE

Haloragis heterophylla
Myriophyllum sp.²

LAMIACEAE

**Marrubium vulgare*
*Mentha diemenica*³
 **Salvia verbenaca*

LINACEAE

Linum marginale

LYTHRACEAE

Lythrum lyssopifolia

MALVACEAE

**Modiola caroliniana*

ONAGRACEAE

Epilobium billardierianum

OXALIDACEAE

Oxalis perennans

PLANTAGINACEAE

**Plantago coronopus*

Plantago gaudichaudii

**Plantago lanceolata*

POLYGALACEAE

Comesperma polygaloides

POLYGONACEAE

Muehlenbeckia cunninghamii
 **Polygonum aviculare*
 **Rumex conglomeratus*
Rumex dumosus

PRIMULACEAE

**Anagallis minima*

ROSACEAE

Acaena echinata
 **Rosa rubiginosa*

RUBIACEAE

Asperula conferta

SCROPHULARIACEAE

**Kickxia elatine* ssp. *crinita*
 **Linaria pelisseriana*
 **Parentucellia latifolia*
Veronica gracilis

SOLANACEAE

**Lycium ferocissimum*

STACKHOUSIACEAE

Stackhousia monogyna

THYMELEACEAE

Pimelea curviflora
Pimelea serpyllifolia

² *Myriophyllum* sp. = *M. propinquum*, sensu Willis (1972)

³ *Mentha diemenica* recorded in 1987 by D. Tonkinson (pers. comm.)

THE SOIL SEED BANK OF A LONG-GRAZED *THEMEDA TRIANDRA* GRASSLAND IN VICTORIA

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The soil seed bank of a remnant *Themeda triandra* grassland was described using the seedling emergence technique. The grassland had been grazed by stock for over 70 years until managed for nature conservation in 1985. Seventeen native species and 24 exotics were recorded in the seed bank, which was dominated by exotics. *Vulpia bromoides* accounted for 61% of germinants and *V. bromoides*, *Romulea rosea* and *Aira cnpaniana* together accounted for 81%. The seed bank contained one native species, *Crassula decumbens*, that was not otherwise known from the reserve and three additional exotics, *Cerastium glomeratum*, *Sagina procumbens* and a *Vicia* species. Species-poor and species-rich *T. triandra* grasslands within the reserve had very similar seed banks, and few of the extra species in the vegetation of the former were present in the soil seed bank. It is suggested that the soil seed banks of long-grazed remnants of *T. triandra* grasslands may contain few native species that are not present in the standing vegetation. In long-grazed *T. triandra* grassland, disturbances that are necessary to maintain the diversity of native species, such as burning, are likely to promote exotic species as much as, if not more than, natives.

TEMPERATE grasslands dominated by *Themeda triandra* are poorly represented in conservation reserves in Australia (Specht 1981) and the best remnants in Victoria are typically small and fragmented on rail and road easements (Stuwe & Parsons 1977, Stuwe 1986). Effective conservation of grassland ecosystems requires the reservation of large areas. However, suitable sites invariably have been grazed by stock for considerable periods of time and, consequently, have relatively low diversities of native species, and many exotics (Stuwe 1986). Many sites from which grazing has recently been removed support dense *T. triandra* (over 90% cover) with few individuals of other species (Stuwe 1986, McDougall 1987).

Typically, the standing vegetation at a particular site is only part of the total flora, and propagules of additional species are stored in the soil, often for periods far longer than the lifespan of established plants. Species present in the soil seed bank may often be promoted by soil or vegetation disturbances such as ploughing or burning (Major & Pyott 1966, Roberts 1981, Fenner 1985, Chancellor 1986). Soil seed banks thus provide the potential for vegetation change.

The 154 ha Derrimut Grassland Reserve, the largest grassland reserve on the basalt plains of western Victoria, was grazed by sheep and cattle for over 70 years until managed for nature con-

servation in 1985. It was studied in order to: (a) provide a general description of the soil seed bank of a previously grazed *T. triandra* grassland now managed for nature conservation; and (b) determine whether native species in the standing vegetation of small patches of species-rich grassland within the reserve were represented in the seed bank of larger areas of species-poor grassland.

METHODS

The Derrimut Grassland Reserve (37°48'30"S, 144°47'40"E) is 14 km west of Melbourne, Victoria. Site characteristics, land use history and a floristic classification of the vegetation are given by Lunt (1990a). Although the reserve contains a number of native grassland and wetland vegetation types, the seed bank study included only grasslands dominated by *T. triandra*. One species-rich site, floristically related to *T. triandra* grassland but classified as *Vulpia bromoides* grassland due to a low cover of *T. triandra* (Lunt 1990a), is referred to *T. triandra* grassland throughout this paper.

In January 1987, soil samples 40 mm deep and 0.25 m² in area were taken next to four of the richest and four of the poorest vegetation quadrats. The mean species richness of the former was 35 species per 15 m² quadrat and of

the latter 11 species per quadrat. Except for one soil sample which could not easily be sieved, samples were passed through a 4 mm² sieve to remove coarse material and recognizable vegetative propagules, particularly corms of *Romulea rosea*. A 10 mm deep layer of each soil sample was spread over potting mix in five seedling trays, each 8.96×10^{-2} m² in area, except for two quadrats for which sieved soil was sufficient for only four trays. Five control trays were filled only with potting mix. Trays were randomly

arranged in an unheated glasshouse for 151 days, from 13 January to 24 May 1987. They were regularly watered and seedlings were removed as identified. Densities of viable seeds were compared statistically by Students t-test (Sokal & Rohlf 1981).

Danthonia and *Isolepis* seedlings were identified only to genus, and in three cases pairs of species were not distinguished (Table 1). *Cyperus tenellus* and *Schoenus apogon* were noted in the field but not as glasshouse germi-

Species	Density (viable seeds per m ²)					
	Species-poor			Species-rich		
	mean	range		mean	range	
* <i>Vulpia bromoides</i>	3199	268	10848	15087	8796	23950
* <i>Romulea rosea</i>	1483	455	3103	2711	170	9497
* <i>Aira cupaniana</i>	128	56	170	1759	45	3509
<i>Juncus bufonius/capitatus</i>	805	112	1786	319	27	786
<i>Themeda triandra</i>	769	447	1375	139	98	241
* <i>Briza maxima/minor</i>	81	0	313	430	9	1149
<i>Wahlenbergia</i> sp.	232	152	304	208	45	304
* <i>Centaureum tenuiflorum</i>	221	71	536	186	45	509
<i>Isolepis</i> spp.	142	22	277	199	0	777
* <i>Sagina procumbens</i>	152	0	591	186	54	509
<i>Danthonia</i> spp.	26	9	54	253	100	643
* <i>Cicendia quadrangularis</i>	47	0	170	147	36	420
<i>Calocephalus citreus</i>	9	0	27	172	0	500
<i>Crassula decumbens</i>	46	22	89	103	0	313
* <i>Gnaphalium purpureum</i>	39	9	67	110	0	402
* <i>Hypochoeris radicata</i>	73	45	125	53	0	107
<i>Oxalis</i> sp.	73	9	212	36	0	98
<i>Juncus subsecundus</i>	9	0	27	70	0	201
* <i>Trifolium campestre/dubium</i>	32	9	71	7	0	11
* <i>Cerastium glomeratum</i>	16	0	54	16	0	36
* <i>Leontodon taraxacoides</i>	14	0	36	10	0	27
<i>Deyeuxia quadriseta</i>	3	0	11	24	0	67
* <i>Lolium rigidum</i>	12	0	22	11	0	44
* <i>Vicia</i> sp.	2	0	9	7	0	18
<i>Helichrysum apiculatum</i>	2	0	9	3	0	11
* <i>Trifolium subterraneum</i>	131	0	473			
* <i>Bromus hordeaceus</i>	84	0	170			
* <i>Trifolium angustifolium</i>	7	0	27			
* <i>Sonchus oleraceus</i>	15	0	22			
<i>Lythrum hyssopifolium</i>	2	0	9			
<i>Leptorhynchus squamatus</i>				14	0	54
<i>Eryngium ovium</i>				5	0	18
* <i>Hainardia cylindrica</i>				3	0	11
<i>Convolvulus crubescens</i>				3	0	11
* <i>Plantago coronopus</i>				3	0	11
<i>Solenogyne dominii</i>				2	0	9
* <i>Erodium</i> sp.				2	0	9
<i>Hypericum gramineum</i>				2	0	9

Table 1. Mean and range of number of viable seeds per m² recorded from species-poor and species-rich *T. triandra* grassland. Species nomenclature follows Forbes & Ross (1988); asterisks denote exotic species.

nants and may have been mistaken for *Isolepis* species. Specimens referred to *Vulpia bromoides* may have included some *Vulpia myuros* forma *megalura*, but most appeared to be of the former species. The *Juncus bufonius/capitatus* group included the native *J. bufonius* and the exotic *J. capitatus*, and equal numbers of both were assumed in native/exotic comparisons.

RESULTS

Excluding glasshouse contaminants, 41 herbaceous species including 17 natives and 24 exotics germinated from the soil seed bank (Table 1). No ferns or woody plants were recorded. Exotics comprised 59% of species but 91% of individuals (Table 2). A small number of species dominated the soil seed bank: *Vulpia bromoides* accounted for 61% of individuals, and the three exotics *V. bromoides*, *Romulea rosea* and *Aira cupaniana* together accounted for 81%. In contrast, 24% of species were represented by only one or two individuals. Four species identified from the seed bank had not previously been recorded from the reserve: one native, *Crassula decumbens*, and three exotics, *Cerastium glomeratum*, *Sagina procumbens* and a *Vicia* species.

For all but three species, the number of viable seeds in species-poor and species-rich *Themeda* grassland was not significantly different ($p > 0.05$). Viable seeds (and established plants) of *V. bromoides* and *Aira cupaniana* were significantly more abundant in species-rich than in species-poor grassland, and viable seeds (and flowering culms) of *T. triandra* were more abundant in species-poor than in species-rich grassland ($p < 0.05$). Thirty species were recorded from the seed bank of species-poor grassland

and 33 from that of species-rich grassland (Table 1). Both seed banks were similar in composition, with 25 species (66% of seed bank species) occurring in both. Of the 22 native species recorded from the vegetation of species-rich but not species-poor grassland, only four appeared in the seed bank of species-poor grassland: *Calocephalus citreus*, *Helichrysum apiculatum*, *Isolepis* species and *Juncus bufonius*.

DISCUSSION

The seed bank of *Themeda triandra* grassland in the Derrimut Grassland Reserve possessed characteristics typical of most seed banks, including high spatial variability, poor correspondence with the standing vegetation, domination by one or two species of annual monocotyledons, and a relatively low representation by perennials (see e.g. Roberts 1970, Donelan & Thompson 1980, Rabinowitz 1981, Reichman 1984, Schenkeveld & Verkaar 1984, Thompson 1986). Its composition was very similar to that of seed banks of annual grasslands in inland California (Heady 1956, 1977, Major & Pyott 1966, Bartolome 1979), due to the abundance of exotic annual grasses, including *Aira*, *Briza* and *Vulpia*. Before these species were introduced, Victorian and inland Californian grasslands were dominated by perennials, *T. triandra* and *Stipa pulchra* respectively (Willis 1964, Heady 1977, Bartolome et al. 1986). Seed densities could not be compared accurately, due to different sampling and germination procedures, but those obtained here (from 4,601 to 28,337 viable seeds per m²) were of the same order of magnitude as those recorded from California (Major & Pyott 1966). Up to 670,000 seeds of *Vulpia bromoides* per m² occurred in dense stands of *Vulpia* in California (Bartolome 1979), and comparable densities might be expected in dense stands of *V. bromoides* at Derrimut.

It has been suggested that the demise of *T. triandra* under grazing may have been caused by an inherently low rate of seed production (Groves et al. 1973, Groves & Williams 1981) but this appears unlikely since, in this study, *T. triandra* was the fifth most abundant species in the seed bank, producing up to 1,375 viable seeds per m².

Species that did not germinate in the glasshouse cannot be presumed absent from the seed bank, since sampling and germination procedures may not have been appropriate for all species. Although sampling intensity was sufficient to indicate general characteristics of the

Group	Individuals		Species	
	Number	%	Number	%
Annuals	10113	80	24	59
Perennials	2496	20	17	41
Exotics	11506	91	24	59
Natives	1103	9	17	41
Monocotyledons	11608	92	15	37
Dicotyledons	1001	8	26	63
Total	12609	—	41	—

Table 2. General characteristics of soil seed bank of a long-grazed *Themeda triandra* grassland.

seed bank, particularly in relation to the life-form and origin of component species, the limited number of samples has undoubtedly under-estimated the total number of species. The abundant germination of two species with contrasting optimal germination temperatures (*Romulea rosea* at 9.5–13°C and *T. triandra* at 20–30°C; Eddy & Smith 1975, Groves et al. 1982) suggests that the variable temperature regime encompasses the requirements of most species. However, species requiring extremely low or high soil temperatures (e.g. hard-seeded Fabaceae) or those with obligate after-ripening requirements were probably undetected or under-represented. Despite these qualifications, the results presented here are supported by a study of post-fire regeneration in the reserve (Lunt 1990b). Following a 21 ha fire in autumn 1987, only 16 of 58 native species in the burnt area regenerated from seed. All but four, *Acaena echinata*, *Agrostis avenacea*, *Spergularia rubra* and a *Stipa* species, were recorded from the soil seed bank.

Despite limited sampling, the soil seed bank appeared to contain few native species that were not known from the standing vegetation. The seed banks of many natives were probably grossly depleted by stock grazing or associated management (e.g. an absence of burning). Given the paucity of additional natives and the preponderance of exotics, Donelan & Thompson's (1980) conclusion that "no help can be expected from the seed bank in any attempt to restore species-rich [English] grassland" may prove to be equally relevant to the management of long-grazed, *T. triandra* grassland.

T. triandra grasslands need to be disturbed frequently, by burning or macropod grazing, to maintain the diversity of native species (Stuwe & Parsons 1977, Robertson 1985, Kirkpatrick 1986, Stuwe 1986). However, the composition of the soil seed bank suggests that disturbances in long-grazed grasslands may promote exotics as much as, if not more than, natives. Grassland ecologists face the formidable task of devising disturbance regimes to promote natives at the expense of exotics. Unfortunately, as in Californian grasslands (Heady 1977, Foin & Hektner 1986), many exotics now appear to be permanent residents of *T. triandra* grasslands.

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POLYCOPIDAE (OSTRACODA) FROM THE LATE TERTIARY OF THE PORT PHILLIP AND WESTERN PORT BASINS, VICTORIA

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WARNE, M. T., 1990:05:31. Polycopidae (Ostracoda) from the Late Tertiary of the Port Phillip and Western Port Basins, Victoria. *Proceedings of the Royal Society of Victoria* 102(1): 59-66. ISSN 0035-9211.

Six polycopid species have been identified from various Late Tertiary lithologies within the Port Phillip and Western Port Basins. One species, *Polyclope sanctacatherinae*, has been previously described; three others, *P. melbournensis*, *P. thomasi* and *P. warneetensis* are described as new. The last has a faint irregular pentagonal network of surface furrows which is an unusual ornament for the Polycopidae. Two further species, *Polyclope* sp. A and *Polycopsis*? sp. A are left under open nomenclature.

AS PART of a research program on the Late Tertiary Ostracoda from the Port Phillip and Western Port Basins (Warne 1986, 1987, 1988, 1989), species belonging to the family Polycopidae are here described. Details of the relationship between total ostracod assemblages, palaeoenvironments and facies within the Late Tertiary sequences as well as key first occurrences of ostracod species is presented in Warne (1989).

Comparison of the Miocene and Pliocene faunas from the Port Phillip and Western Port Basins with Late Eocene to Pleistocene ostracod faunas from elsewhere in Victoria (Davies 1985, Guzel 1984, McHenry 1983, Warne 1982, Woodall 1986) indicates that the late Early to early Middle Miocene rocks contain a high diversity of polycopid species. These rocks also yield a high percentage of strongly ornamented forms, suggesting comparatively warm aquatic conditions at the time of deposition (McKenzie & Peypouquet 1984).

MATERIAL AND LOCALITIES

Outcrop samples of approximately 0.5 kg dry weight were collected from the Fyansford Formation in the Batesford Limestone Quarry and at Fossil Beach, Mornington; the Sherwood Formation at Flinders and in boreholes on French Island and near Tyabb, Warneet, Koo-wee-rup and Lang Lang; and from the "Warneet Sands" in Geological Survey of Victoria Sherwood No. 18 bore near Warneet, Western Port. These localities are shown on the maps of Warne (1988, figs 1-3) who also summarised the lithostratigraphy of the region. The localities range in age from late Early Miocene to late Late Miocene or Early Pliocene and yield ostracod faunas

belonging to PA1 to PA5 (palaeoenvironmental/age associations of Warne 1987).

Type and figured specimens are housed in the invertebrate palaeontological collections of the Museum of Victoria under the registered numbers NMV P122190-P122201. Other specimens are housed on assemblage slides under the registered numbers NMV P122682-P122763. Locality details for assemblage slides are recorded at the Museum of Victoria.

The abbreviations RV = right valve, LV = left valve, L = length, H = height are used throughout the text.

SYSTEMATIC PALAEONTOLOGY

Subclass OSTRACODA Latreille, 1806
Order MYODOCOPIDA Sars, 1866
Suborder CLADOCOPA Sars, 1866
Family POLYCOPIDAE Sars, 1866

Remarks. Chavtur (1977, 1979, 1981) arranged Recent polycopids into sixteen genera based on differences in soft part anatomy, but the relationship between these differences and carapace morphology is unclear. Prior to Chavtur's classification Cainozoic polycopids had been assigned to the four genera *Polyclope* Sars, 1866, *Polycopsis* Müller, 1894, *Parapolycope* Klie, 1936 and *Metapolycope* Kornicker & van Morkhoven, 1976. This earlier classification is employed herein although there are also uncertainties with this scheme relating to the significance of carapace morphology. Neale (1983) noted that *Polyclope* and *Parapolycope* cannot be distinguished on carapace morphology alone, and considered that the distinction between *Polyclope* and *Polycopsis* may not be justified if soft parts are unknown. Polycopid taxonomy

was further complicated by Bonaduce et al. (1980) who included specimens attributed to the type species of *Polycopsis* in *Metapolycope*.

Genus *Polycope* Sars, 1866

Type species. Polycope orbicularis Sars, 1866.

Remarks. The five *Polycope* species described herein fall into two morphological groups. Group 1, which is characterised by narrow inner lamellae, no division of the muscle scars and relatively strongly ornamented carapaces, includes *P. sanctacatherinae* Whatley & Downing, 1983, *P. melbournensis* sp. nov. and *P. sp. A*. Group 2, characterised by broad inner lamellae, division of the posterior and dorsal scars in some specimens and weakly ornamented carapaces, includes *P. thomasi* sp. nov. and *P. warneetensis* sp. nov. Group 2 species also have greater valve overlap in the dorsal region and thicker hinge elements than group 1 species. These two groups show a broad correla-

tion with palaeodepth, group 1 species tending to be more abundant in deeper-water facies than group 2 species (Warne 1987).

Polycope sanctacatherinae Whatley & Downing, 1983

Figs 1A, 2A-D

Polycope sp.—McKenzie 1974: 160, pl. 1, fig. 1.
Polycope sanctacatherinae Whatley & Downing 1983: 387–388, pl. 8, figs 20–21.—Warne 1987: 441, pl. 1, fig. A.

Holotype. Adult RV, OS 121000 from the Fyansford Formation (Middle Miocene, Balcombian) at Fossil Beach, Mornington, Victoria; housed in the Micropalaeontology Section, Department of Geology, University College of Wales, Aberystwyth.

Additional material. One hundred and three disarticulated adult and juvenile valves from the Fyansford and Sherwood Formations.

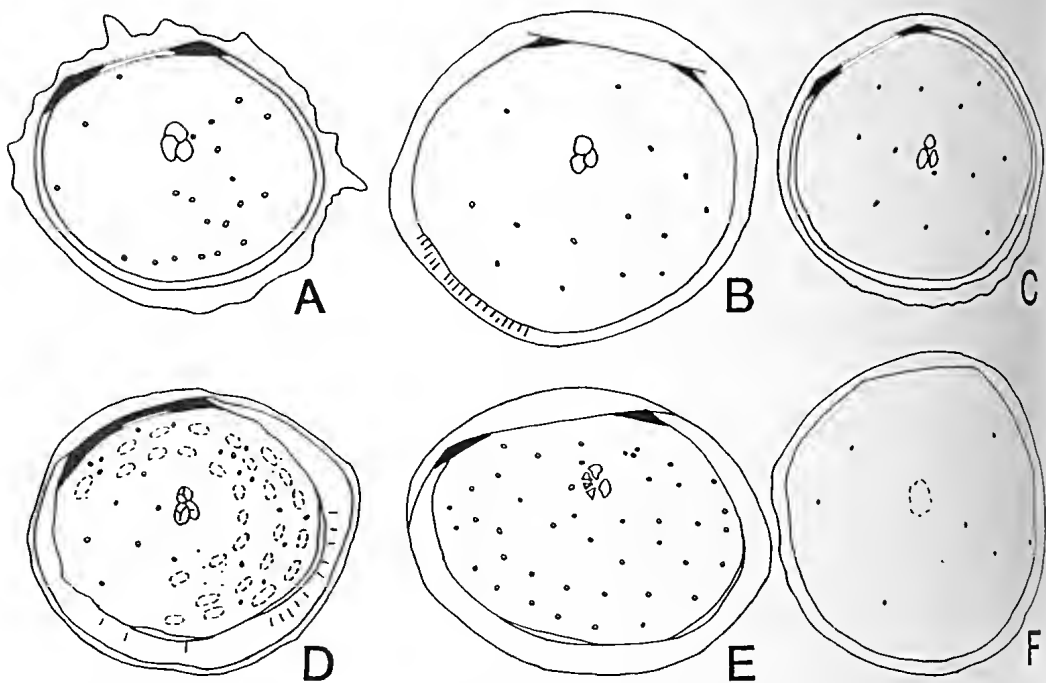


Fig. 1. A, *Polycope sanctacatherinae* Whatley & Downing, 1983, LV internal, NMV P122191, $\times 122$. B, *Polycope melbournensis* sp. nov., RV internal, NMV P122195, paratype, $\times 90$. C, *Polycope* sp. A, LV internal, NMV P122200, $\times 116$. D, *Polycope thomasi* sp. nov., LV internal, NMV P122196, holotype, $\times 130$. E, *Polycope warneetensis* sp. nov., LV internal, NMV P122198, holotype, $\times 85$. F, *Polycopsis*? sp. A, RV internal, NMV P122201, $\times 81$. A–C from Fyansford Formation (Balcombian), Fossil Beach, Mornington; D from Fyansford Formation (Balcombian), Batesford Limestone Quarry; E, F from “Warneet Sands” (Cheltenhamian or Kalimnan), Geological Survey of Victoria Sherwood 18 borehole.

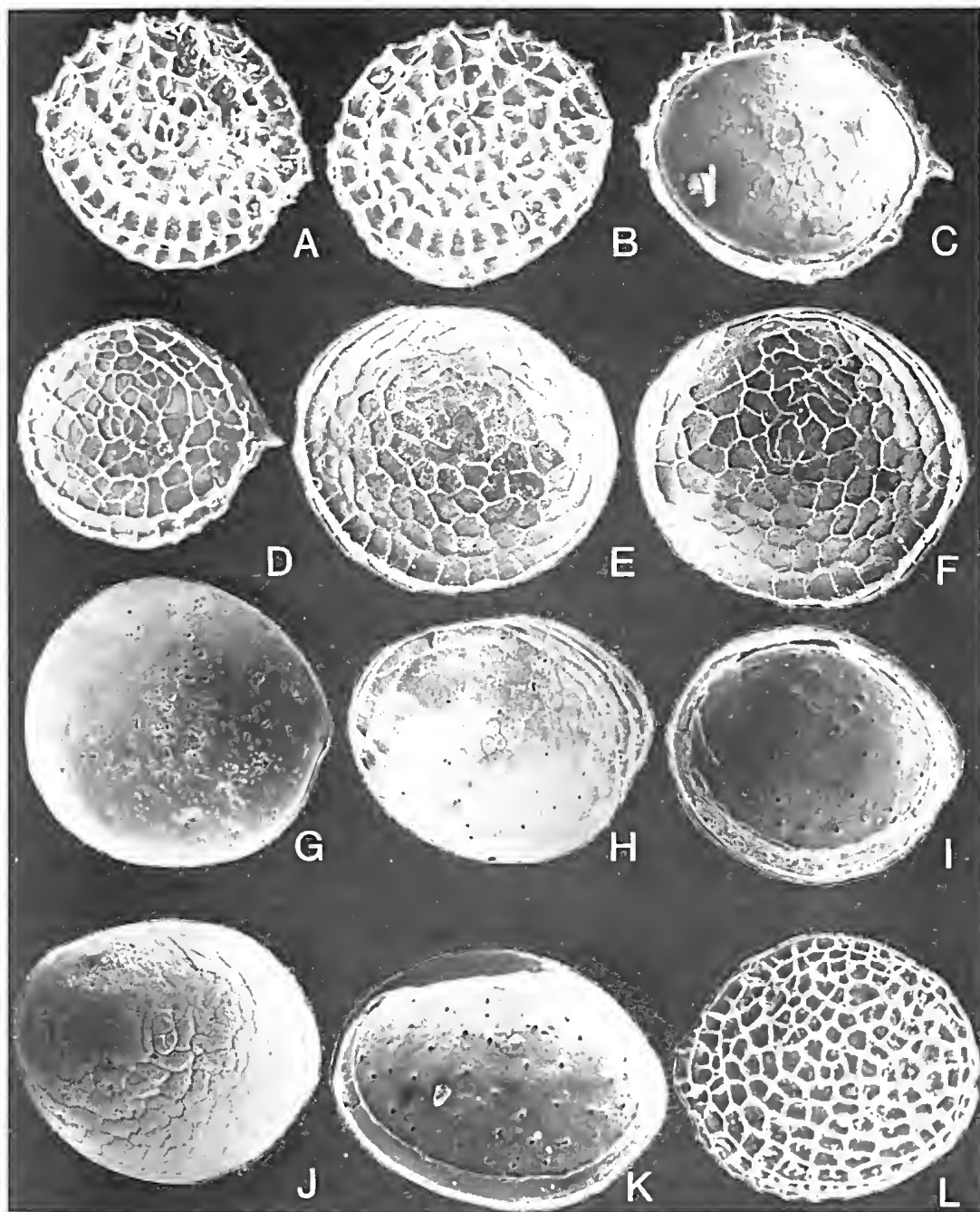


Fig. 2. A–D, *Polycope sanctacatherinae* Whatley & Downing, 1983. A, LV external, NMV P122190, $\times 117$. B, RV external, NMV P122192, $\times 119$. C, LV internal, NMV P122191, $\times 125$. D, RV external, juvenile, NMV P122193, $\times 175$. E, F, *Polycope melbournensis* sp. nov. E, LV external, NMV P122194, holotype, $\times 85$. F, RV external, NMV P122195, paratype, $\times 94$. G, *Polycopsis* sp. A, RV external, NMV P122201, $\times 78$. H, I, *Polycope thomasi* sp. nov. H, RV external, NMV P122197, paratype, $\times 148$. I, LV internal, NMV P122196, holotype, $\times 138$. J, K, *Polycope warneetensis* sp. nov. J, RV external, NMV P122199, paratype, $\times 78$. K, LV internal, NMV P122198, holotype, $\times 78$. L, *Polycope* sp. A, LV external, NMV P122200, $\times 120$. A–F, L from Fyansford Formation (Balcombian), Fossil Beach, Mornington; G, J, K from “Warneet Sands” (Cheltenhamian or Kalimnan), Geological Survey of Victoria Sherwood 18 borehole; H, I from Fyansford Formation (Balcombian), Batesford Limestone Quarry.

Dimensions. LV, NMV P122190: L = 0.36 mm, H = 0.29 mm; LV, NMV P122191: L = 0.36 mm, H = 0.29 mm; RV, NMV P122192: L = 0.37 mm, H = 0.30; juvenile RV, NMV P122193: L = 0.24 mm, H = 0.19 mm.

Remarks. This species is very similar to *Polycope* sp. 1 Whatley & Downing, 1983 (= *Polycope* sp. 3 Warne, 1987) but there are minor differences in size, ribbing and reticulation. The possibility that the two forms are variants of the one species is not excluded. *Polycope demulderi* Sissingh, 1972 and the species illustrated by Puri & Hulings (1976) as *Polycope? favius* Brady, 1880 (although somewhat different from the illustration of this species in Brady's monograph) are probably closely related forms because of their similar shape and ornamental pattern. Chavtur (1981) tentatively included *P. demulderi* in his genus *Archypolycope* which is, however, defined on soft part anatomy (see discussion of family above).

Age and stratigraphical range. Recorded only from the early Middle Miocene (Balcombian to early Bairnsdalian, foraminiferal zones N8/9–N10/11) clays of the Fyansford and Sherwood Formations.

Polycope melbournensis sp. nov.

Figs 1B, 2E–F

Polycope sp. 1.—Warne 1987: 441, pl. 1, fig. B.

Polycope sp. 5.—Warne 1987: 441.

Etymology. A reference to the city of Melbourne, situated in the northern part of the Port Phillip Basin.

Holotype. Adult LV, NMV P122194 from the Fyansford Formation (Middle Miocene, Balcombian) at mid tide level, Fossil Beach, Mornington, Victoria, approximately 200 m north of end of driveway down to beach; 38°14'S, 145°02'E.

Paratype. Adult RV, NMV P122195.

Additional material. Fifty-one disarticulated adult and juvenile valves from the Fyansford and Sherwood Formations.

Dimensions. Holotype, LV, NMV P122194: L = 0.55 mm, H = 0.46 mm; paratype, RV, NMV P122195: L = 0.52 mm, H = 0.47 mm.

Diagnosis. Carapace moderately large, with loosely ordered reticulum and prominent anterior and anteroventral marginal rib parallel to free margin.

Description. Carapace thin-shelled, inflated posterodorsally. RV larger than LV, both valves more or less circular in shape. RV with a very weakly developed anterior rostrum, not evident in LV. Dorsal margin short, slightly arched in RV, straight in LV; posterior margin of both valves evenly rounded; anterior margin straight in anteroventral region of RV. In dorsal view both valves slightly swollen posteriorly. Maximum length at mid-height; maximum height at mid-length; maximum width slightly posterior to and above mid-height. Low relief ornament covering most of carapace, consisting of pentagonal reticulæ on periphery and a distinct anterior and anteroventral marginal rib parallel and close to free margin. Normal pore canals large, simple and scattered. Inner lamellæ narrow with inner margin parallel to outer margin. No vestibule visible; marginal pore canals seen in posterior region are numerous and straight. Hinge simple, smooth and adont. A series of small anteroventral denticles present on both valves. Adductors consisting of a cluster of three scars at maximum width of carapace. Sexual dimorphism not conspicuous though some adults are very slightly more inflated than others and these may be females.

Remarks. Differences in the degree of ornamental relief in *P. melbournensis* were originally interpreted by me (Warne, 1987) as indicating the presence of two different species, but these differences seem to be due to either ecophenotypic or taphonomic factors. *P. melbournensis* is similar to *P. reticulata* Müller, 1894 but the latter is slightly different in shape and has a more strongly developed and irregularly shaped reticulum. *P. cancellata* Hartmann, 1954 is smaller and possesses a less evenly rounded lateral outline. *Pseudopolycope intermedia* (Chavtur, 1979) has a more angular dorsal margin and lacks a marginal ridge. *Pseudopolycope krytatchki* (Chavtur, 1977) differs in having a lateral protuberance, whereas *Pseudopolycope comandorica* Chavtur, 1979 is larger and has a more clearly defined rostrum. The similarities between *Polycope melbournensis* and the last three species suggest, however, that the new species may be referred ultimately to *Pseudopolycope*.

Age and stratigraphical range. Specimens range in age from late Early Miocene (Batesfordian, foraminiferal zones N7/8) to late Middle or early Late Miocene (late Bairnsdalian or Mitchelian?), occurring in marls, clays and sands of the Fyansford and Sherwood Formations.

***Polycope thomasi* sp. nov.**

Figs 1D, 2H-I

Polycope, sp. 2.—Warne 1987: 441.*Etymology.* In recognition of Dr G. A. Thomas, palaeontologist.*Holotype.* Adult LV, NMV P122196 from near the top of the Fyansford Formation (Middle Miocene, Balcombian) in the south-west face of Batesford Limestone Quarry, near Fyansford, Victoria (base of upper quarry bench well above the upper limit of *Lepidocyclina* sp., approximately 25 m above boundary with Batesford Limestone); 38°06'S, 144°17'E.*Paratype.* Adult RV, NMV P122197.*Additional material.* Seven disarticulated adult and juvenile valves from the Fyansford Formation.*Dimensions.* Holotype, LV, NMV P122196: L = 0.32 mm, H = 0.27 mm. Paratype, RV, NMV P122197: L = 0.30 mm, H = 0.26 mm.*Diagnosis.* Carapace very small, subrounded, smooth except for faint dorsal and anterodorsal ridges adjacent and parallel to outer margin; series of rounded opaque (patch) patterns evident, dense near free margin but sparser in central and dorsal regions.*Description.* Carapace thin. LV slightly larger than RV and overlapping it dorsally; both valves subrounded and produced anterodorsally with a distinct rostrum. Dorsal margin slightly arched in LV, straight in RV. Maximum length at mid-height; maximum height anterior of mid-length; maximum width at mid-length and slightly above mid-height. Surface ornament consisting of faint marginal ribs, most numerous anterodorsally. Faint peripheral reticulate ornament visible, particularly near posterior and ventral margins. Carapace almost smooth centrally. Normal pore canals simple and scattered. Inner lamellae relatively broad with small vestibules developed in ventral region of both valves. Marginal pore canals straight and irregularly spaced. Hinge short and adont, thicker terminally than in mid-section. Very fine anteroventral denticulation. Adductors consisting of three subrounded scars in a subtriangular cluster located slightly below position of maximum width. Sexual dimorphism not detected.*Remarks.* A few specimens have divided posterior and dorsal adductor scars. In these speci-

mens the overall pattern consists of up to six individual scars and is reminiscent of that of *Metapolycope* species, though not as complex. *P. thomasi* differs from the other species described here in its smaller size. *P. denticulata* Bonaduce et al., 1980 and *P. parvula* Bonaduce et al., 1980 are similar to *P. thomasi* in size but lack the marginal ribbing and conspicuous anterior rostrum. *P. microdispar* Hartmann, 1954 is smaller than *P. thomasi* and possesses a narrower inner lamellae, whereas *P. arenicola* Hartmann, 1954 is larger and slightly more elongate. *Eupolycope kurilensis* (Chavtur, 1977), *E. pellucida* Chavtur, 1979, *Polycopetta curva* Chavtur, 1979, *Micropolycope angulata* (Chavtur, 1977) and *M. paramushiri* (Chavtur, 1977) all resemble *P. thomasi* in their relatively small size, presence of an anterior rostrum and relatively broad inner lamellae, but have muscle scar patterns consisting of three adductors, except *M. paramushiri* which has a pattern of five scars.

Age and stratigraphical range. Recorded only from the early Middle Miocene (Balcombian, formamiferal zones N8/9) clays near the top of the Fyansford Formation in the Batesford Limestone Quarry.***Polycope warneetensis* sp. nov.**

Figs 1E, 2J-K

Polycope, sp. 6.—Warne 1987: 441.*Etymology.* A reference to the type horizon.*Holotype.* Adult LV, NMV P122198 from the "Warneet Sands" (late Late Miocene or Early Pliocene, Cheltenhamian or Kalimnan) in the Geological Survey of Victoria Sherwood 18 borehole, between depths 20 m and 22 m. 38°12'S, 145°16'E.*Paratype.* Adult RV, NMV P122199.*Additional material.* Nine disarticulated adult and juvenile specimens from the type locality.*Dimensions.* Holotype, LV, NMV P122198: L = 0.55 mm, H = 0.44 mm. Paratype, RV, NMV P122199: L = 0.56 mm, H = 0.46 mm.*Diagnosis.* Carapace of medium size, oval, with relatively long dorsal margin, a weakly developed anterior rostrum in both valves and a faint irregular pentagonal network of surface furrows.

Description. Carapace moderately thick, almost equivalved except that LV strongly overlaps RV dorsally. Dorsal margin straight, reaching slightly over half maximum length in both valves. Maximum length at mid-height; maximum height anterior to mid-length; maximum width at mid-length and slightly above mid-height. Outline in dorsal view oval. Surface ornament consisting of faint pentagonal network of furrows giving carapace a scaly appearance. Normal pore canals large, simple and scattered. Inner lamellae relatively broad with small vestibules developed in ventral region of both valves. Marginal pore canals not seen. Hinge simple, smooth and adont, thicker terminally than in mid-section. Adductors consisting of three subtriangular to subrounded scars in a tight cluster at position of maximum width. Posterior and dorsal adductor scars divided in some specimens. Sexual dimorphism not detected.

Remarks. This species is distinguished from *P. melbournensis* by its impressed rather than raised ornament and by its distinctly different shape. Specimens of *P. warneetensis* with divided adductors have a similar muscle scar pattern to *Micropolycope paramushiri* (Chavtur, 1977) but are otherwise quite different. I previously (Warne 1987) attributed to this species some poorly preserved juvenile specimens from the Sherwood Formation, but I now consider that these cannot be definitively assigned to *P. warneetensis*.

Age and stratigraphical range. Recorded only from the late Late Miocene or Early Pliocene (Cheltenhamian or Kalimnan) "Warneet Sands" (Warne, 1987).

Polycope sp. A

Figs 1C, 2L

Polycope sp. 4.—Warne 1987: 441.

Material. Five disarticulated adult and juvenile valves from the Fyansford and Sherwood Formations.

Dimensions. LV, NMV P122200: L = 0.38 mm, H = 0.32 mm.

Description. Carapace of medium size, relatively thick-shelled, irregularly rounded and produced anteroventrally. Dorsal margin gently arched. Maximum length slightly below mid-height; maximum height and width at mid-length.

Strong reticulate ornament comprising six concentric rows between ventral margin and muscle scar region, not as well ordered elsewhere on carapace. Denticulate anteroventral margin. Hinge short, smooth and adont. Inner margin narrow with no vestibules evident. Adductors consisting of three subrounded scars in a tight subtriangular cluster located at position of maximum width. Normal and marginal pore canals not seen. Sexual dimorphism not detected.

Remarks. This is a distinctive species but adult left and right valves have only been found in separate samples. It differs from *P. sanctacatherinae* in lacking distinct ribbing. The reticulation is coarser than in *P. orbulinaeformis* Breman (tentatively placed in *Archypolycope* by Chavtur, 1981).

Age and stratigraphical range. Recorded only from the early Middle Miocene (Balcombian to early Bairnsdalian, foraminiferal zones N8/9–N10/11) clays of the Fyansford and Sherwood Formations.

Genus Polyopsis Müller, 1894

Type species. *Polycope compressa* Brady & Robertson, 1869.

Polyopsis? sp. A

Figs 1F, 2G

Material. One adult valve from the "Warneet Sands" at the same locality as the types of *Polycope warneetensis*.

Dimensions. RV, NMV P122201: L = 0.55 mm, H = 0.48 mm.

Remarks. The carapace is large, smooth, rounded in lateral view and has a weakly developed anterior rostrum. The species is similar to *Polycope quadridentata* Bonaduce et al., 1975 in shape and in being compressed laterally in dorsal view, but it is larger and lacks marginal denticulation. The adductor muscle scar pattern is obscure, and so the possibility that the species belongs to *Metapolycope* cannot be discounted.

Age and stratigraphical range. Recorded only from the late Late Miocene or Early Pliocene (Cheltenhamian or Kalimnan) "Warneet Sands" (Warne, 1987).

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WATER VAPOUR FLUX IN THE EGGS OF TWO SPECIES OF RAIL (RALLIDAE) DURING INCUBATION

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Swamp-dwelling purple swamphens and dusky moorhens lay their eggs in shallow, open nests, typically built of reeds, placed a few centimetres above water level and consequently sometimes noticeably damp. Nest humidity and egg water vapour flux parameters were measured to determine the extent to which the eggs of these species have a water balance problem during incubation. Mean water vapour pressures in the nest were comparatively high (3.6–3.7 kPa). Calculated incubation temperatures averaged 36–37°C and consequently the water vapour pressure gradient across the eggshell was fairly shallow (2.5–2.6 kPa); however, these values were not sufficient to cause a significant water flux problem in the egg. The egg's mean rate of water loss (185–188 mg.day⁻¹), fractional mass loss during incubation (12–13%), water vapour conductance (71.43–74.36 mg (day.kPa)⁻¹) and total functional pore area (1.04–1.15 mm²) all conformed with allometric predictions based on the ratio of egg mass:incubation period. Despite their nest placement and nesting habits, the two species do not exhibit the wet-nesting syndrome typical of some freshwater birds such as grebes and loons.

MOST bird eggs lose 12–18% of their initial mass as water vapour during the incubation period, mainly by diffusion through microscopic pores in the shell. This is crucial in promoting optimal hatching success. The rate of water loss is determined by the water vapour pressure difference across the shell (ΔP_{H_2O}) and its water vapour conductance (G_{H_2O} , in mg (day.kPa)⁻¹). G_{H_2O} is governed by the number, size and length of the pores (Ar & Rahn 1980). Although this gas flux system is now well understood, ecologically-induced, atypical patterns of egg water content regulation remain of great interest.

Water vapour pressure in the nest (P_n) of birds breeding in a wide variety of conditions averages about 2.7 kPa (Walsberg 1980), but the nest microclimate of some grebes (Podicipedidae), loons (Gaviidae) and megapodes (Megapodiidae) is significantly more humid (Scymour & Rahn 1978, Sotherland et al. 1984, Ar & Rahn 1985). Nonetheless, the eggs of these so-called "wet-nesters" maintain an optimal state of hydration during incubation through having such features as a plastron-like outer shell structure resistant to liquid water influx (Board 1982, Sotherland et al. 1984), or a greatly elevated G_{H_2O} (Ar & Rahn 1985). However, the extent and causes of the wet-nesting syndrome, and

variations in this phenomenon, are still poorly documented.

In eastern Australia, the dusky moorhen, *Galinula tenebrosa*, and purple swamphen, *Porphyrio porphyrio*, commonly nest in dense reed beds in the same wetlands. Their nests are shallow bowls, made of reeds and rushes (although moorhens sometimes use twigs and bark) and often placed only a few centimetres above water level (Beruldsen 1980). Some nests are noticeably damp at times due to short-term water level fluctuations, condensation "run-off" from the dense surrounding vegetation and from moisture transported on the incubating adults' body. Both species are therefore potentially wet-nesters. This investigation examined whether the microclimate of moorhen and swamphen nests is unusually humid and, if so, whether this generates any water balance problem in the egg.

METHODS

Field data were obtained from September–December in several years from 7 locations within 150 km of Melbourne, including Healesville, Coldstream, Werribee and Heidelberg. During these months, Melbourne has an average relative humidity of 60–68% and average daily maximal and minimal temperatures of about

17–25°C and 6–14°C respectively. Eggs were collected under permit from four of the sites for experimental work. Nesting habitat comprised artificial and natural ponds, dams, lakes and marshes, often with emergent stands of *Typha* sp. and *Eleocharis* sp.

The initial mass of eggs (± 0.01 g) was determined: (a) by weighing newly-laid eggs in the field on a wind-shielded Shinko Denshi portable balance, and (b) for a further sample of partly developed eggs, by estimation from their linear dimensions (± 0.05 mm), using the equation

$$W = K_w \times LB_{\max}^2 \text{ (Hoyt 1979),}$$

where W is fresh mass (g), L is length, B_{\max} is maximum breadth (mm) and K_w is a species-typical constant which was empirically determined for both species.

The mean daily mass loss of incubated eggs at various stages of development was determined by marking them with indelible ink and weighing them (as above) at intervals of 5–22 days. Since nearly all mass loss can be attributed to water vapour loss (Drent 1970, Rahn & Ar 1974), this value equals the mean daily rate of water loss (M_{H_2O} , in $\text{mg}\cdot\text{day}^{-1}$).

Nest humidity was determined by the method of Rahn et al. (1977a). The gain in mass of hygrometer eggs (consisting of eggshells fitted with metal screw caps and filled with dry silica gel) when placed in active nests for periods of 2–4 days was divided by their water vapour conductance. The latter quantity was determined by measuring their mean daily mass gain at 20°C and 76% RH in the laboratory over a 4 day period.

G_{H_2O} of intact eggs was determined by the method of Ar et al. (1974). The daily weight loss (± 1 mg) of eggs placed over dry silica gel in a desiccator at 20°C was measured over 8–9 days. Values obtained were corrected to a barometric pressure of 101.33 kPa and also to a temperature of 25°C to facilitate interspecific comparisons. Determinations were mostly done on fresh eggs, but a few older eggs were included to give an indication of whether shell conductance increased markedly during incubation, as reported for a few bird species (Carey 1979).

Shell parameters influencing the egg's G_{H_2O} were measured on dried shells which were cut with a dental drill with a cutting bit into equatorial, pointed and blunt pole sections. True shell thickness (L) and pore density were measured on 12 equatorial and 6 polar (3 from each pole) fragments from each egg. The fragments were first briefly boiled in 5% NaOH to remove the shell membranes. L (± 1 μm) was measured with a

Tesa dial micrometer fitted with an hemispherical anvil to accommodate the curvature of the shell. Pore density was determined for the same fragments by painting the inner surface with acid fuchsin, which penetrated the pores so that they could be detected as discrete spots on the outer surface (Ar & Rahn 1985). The fragments were mounted on a Nikon V20A Profile Projector and the number of pores in a 25 mm² area counted from the magnified ($\times 20$) image. For each species, the number of pores in an egg of average size (N) was calculated as the product of mean pore density and surface area, which was estimated from equation (12) of Hoyt (1976). Pore shape and form were examined by viewing platinum-coated, radial sections of shell under an Hitachi S570 SEM.

The relative magnitude of egg water vapour flux parameters in swamphens and moorhens was assessed by comparing observed values with those predicted from egg mass/incubation period (M/I) (relative embryonic growth rate) using established regression equations based on data for many species (sources in Table 1).

RESULTS

Egg size measurements and mean values for egg parameters which influence its water vapour flux are summarised for both species in Table 1.

In the purple swamphen, P_n averaged 3.7 ± 0.4 kPa (range 2.9–4.1 kPa; $n = 16$ determinations for 10 nests); only three values were less than 3.5 kPa. 36.3 g, the average of the two estimates derived respectively by weighing and from dimensions, was taken as the best estimate of mean initial egg mass. At the mean M_{H_2O} observed, an egg of this mass would have an estimated fractional mass loss of c. 12% over the 24 day incubation period. G_{H_2O} corrected to 25°C ranged from 60.23 to 102.63 $\text{mg}\cdot(\text{day}\cdot\text{kPa})^{-1}$; the mean values for the three older eggs and the nine fresh eggs, which had equivalent mean initial masses, were not significantly different (75.65 ± 12.61 versus 70.60 ± 11.24 $\text{mg}\cdot(\text{day}\cdot\text{kPa})^{-1}$; $t_{110} = 0.613$, $p > 0.05$). The mean ΔP_{H_2O} in the nest was 2.5 kPa. The mean saturated vapour pressure of the egg contents was therefore 6.1 kPa, which translates into a mean incubation temperature of 36–37°C. Pore density averaged 28 ± 10 , 25 ± 8 and 35 ± 8 pores per 25 mm² at the pointed pole, equator and blunt pole respectively.

In the dusky moorhen, P_n averaged 3.6 ± 0.4 kPa (range 2.9–4.2 kPa; $n = 11$ determinations

Parameter	Swamphen		Ratio observed: predicted means	Moorhen		Ratio observed: predicted means
	Observed mean			Observed mean		
Length (mm)	52.12 ± 2.19	(53;16)		50.55 ± 2.49	(20;6)	
Max. breadth (mm)	36.41 ± 0.91	(53;16)		35.03 ± 1.52	(23;8)	
Initial mass (g)	35.14 ± 3.25	(31;13)		33.42 ± 2.89	(21;7)	
Estimated initial mass (g)	37.45 ± 2.80	(45;10)		33.82 ± 4.39	(14;4)	
I (days)	24			24		
M _{H₂O} (mg.day ⁻¹)	185 ± 38	(61;13)	0.83	188 ± 35	(136;16)	0.91
G _{H₂O} (mg.[day.kPa] ⁻¹)	74.36 ± 12.03	(12;11)	1.30	71.43 ± 16.09	(15;12)	1.35
L (μm)	235	(20;15)	0.85	270	(12;10)	1.02
N	6087	(20;15)	1.18	5132	(12;10)	1.07
A _p (mm ²) ^a	1.04		1.33	1.15		1.38

^a "observed" value calculated from measured G_{H₂O} and L

Table 1. Size and water vapour flux parameters of rail eggs. Numbers in parentheses are sample sizes of (eggs; nests). I = incubation period; M_{H₂O} = daily rate of water loss; G_{H₂O} = water vapour conductance; L = shell thickness; N = pores per egg; A_p = total effective pore area. Mean K_w used to obtain initial egg mass estimate was 0.541 (swamphen) and 0.539 (moorhen). Estimates of I based on personal observations and on Falla et al. (1985), Garnett (1978), O'Grady & Lindsey (1979), National Photographic Index (1985) and Williams (1966). Sources for predictions: M_{H₂O}, Ar & Rahn (1980); G_{H₂O}, L and N, Ar & Rahn (1985); A_p, Ar & Rahn (1978); predictions based on egg mass/incubation period.

for 6 nests); only three values were less than 3.5 kPa. Mean initial egg mass, derived as for the swamphen, was 33.6 g. At the mean M_{H₂O} recorded, an egg of this mass would have a fractional mass loss of about 13% over the 24 day incubation period. G_{H₂O} corrected to 25°C ranged from 46.24 to 107.02 mg.(day.kPa)⁻¹; the mean conductances of three older eggs with an average initial mass of 32.3 g and nine fresh eggs with an average mass of 34.9 g did not differ significantly (77.67 ± 9.02 versus 69.25 ± 20.08 mg.(day.kPa)⁻¹; *t*₍₁₀₎ = 0.686, *p* > 0.05). ΔP_{H₂O} was calculated to be 2.6 kPa and the mean saturated vapour pressure of the egg contents was therefore estimated to be 6.2 kPa, which translates into a mean incubation temperature of 36–37°C. Pore density of the shell averaged 26 ± 8, 25 ± 6 and 31 ± 8 pores per 25 mm² at the pointed pole, equator and blunt pole respectively. Pores were unbranched, had open orifices and were mostly posthorn-shaped.

DISCUSSION

Given the prevailing ambient temperatures and relative humidities in the study region (see Methods), mean water vapour pressure in the nests of both rails must have been substantially above environmental levels. The calculated mean saturated vapour pressure of the egg contents of the two species was similar to that reported for many other bird species (Walsberg 1980, Rahn 1984) and translates into a mean incubation temperature which is fairly typical of

many birds that maintain a high incubation constancy (Drent 1972). Mean P_n in both species was substantially higher than the averages reported for a large sample of bird species breeding in a variety of environments (2.0–2.8 kPa; Rahn et al. 1977a, Ar & Rahn 1978, Walsberg 1980, Rahn 1984). Mean ΔP_{H₂O} was substantially smaller than the mean values calculated for many other bird species nesting in various environments (3.6–4.7 kPa; Rahn & Ar 1974, Rahn et al. 1977b, Ar & Rahn 1978, 1980, Walsberg 1980, Rahn 1984).

However, P_n and ΔP_{H₂O} were clearly not so unusual as to necessitate any significant compensatory changes in G_{H₂O} or the shell parameters that influence it. Mean values obtained for these factors all lie within the 95% confidence limits of the values predicted by the allometric equations referred to in Table 1. In acknowledged wet-nesters, such as grebes and brush turkeys, where P_n is much higher (4.3–6.4 kPa) and ΔP_{H₂O} much smaller than in the rails, G_{H₂O} and N usually exceed allometrically predicted values by more than two standard errors of estimate (Seymour & Rahn 1978, Davis et al. 1984, Ar & Rahn 1985). This contrast clearly occurs because the eggs of grebes and brush turkeys, unlike those of swamphens and moorhens, are permanently or intermittently covered by warm, moist vegetation, and the eggs of grebes are also often in contact with liquid water.

Comparative data on egg water vapour flux for other rail species are few. M_{H₂O} and N are as expected from egg mass in the king rail, *Rallus*

elegans, and grey moorhen, *Gallinula chloropus*, respectively (Meanly 1969, Ar & Rahn 1985). However, M_{H_2O} is significantly (30–31%) lower than expected in the Sora rail, *Porzana carolina* (Drent 1970), and G_{H_2O} is 87% greater than would be predicted from egg mass in the Eurasian coot, *Fulica atra* (Lomholt 1976). In the American coot, *Fulica americana*, P_n is not particularly elevated (2.4 kPa) and G_{H_2O} accords with allometric predictions; the egg has a standard fractional mass loss during incubation, yet M_{H_2O} is 17–21% less than would be expected on allometric grounds (Drent 1970, Davis et al. 1984).

Much more work is required before the incidence of wet-nesting in the Rallidae can be fully assessed. Clearly, however, the purple swamphen and dusky moorhen, despite their nesting habits, do not exhibit the wet-nesting syndrome typical of some other freshwater birds with similar nest placement, such as grebes and loons.

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ECOLOGY OF RAINFOREST AND SCLEROPHYLLOUS COMMUNITIES IN THE MITCHELL RIVER NATIONAL PARK, GIPPSLAND, VICTORIA

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A survey of the floristics and soils was conducted in a 143 hectare area within the Mitchell River National Park, Victoria, where rainforest patches occur amid sclerophyllous communities. These rainforest patches are amongst the most south-westerly expression of "tropical" elements in Australia. Computer sorting of the survey data delineated six major community types, ranging from undisturbed and disturbed rainforest to wet and dry sclerophyll communities. The topography of the site and disturbance regimes were the major factors delimiting these community types. Undisturbed rainforest patches were restricted to fire protected niches while the floristic composition and structure of sclerophyllous communities appeared to be determined by a combination of site insolation (moisture), fire susceptibility and previous land clearing activities. Although soil chemical properties varied across the site, edaphic factors were regarded as being of secondary importance to topography and disturbance in delimiting the plant communities.

THE FLORA of Gippsland has long been recognized as an unusual melange of community types, varying from dry sclerophyll woodland through to outliers of warm temperate rainforest. This mixture of vegetation types is thought to result from the mild climate, erratic rainfall and history of disturbance in this region (Patton 1930, Land Conservation Council 1985). In one of the earliest floristic descriptions of East Gippsland, Patton (1930) was intrigued by the occurrence of "tropical" and warm temperate species of trees, lianes and even an isolated community of the palm *Livistona australis*, together with eucalypts such as *Eucalyptus polyanthemos* at the eastern limit of their distribution. The coexistence of these species led him to describe East Gippsland as "a meeting ground of two floras; tropical rain flora with a dry sclerophyll flora."

At their southwestern-most limit in East Gippsland, warm temperate rainforests are found only in isolated pockets on a sheltered arm of Lake King, along the Mitchell River gorge and in one of the headwaters of the Freestone Creek at Mt Moornapa (Ashton & Frankenberg 1976, Cameron 1984). The flora of these western pockets is somewhat depleted in comparison with the rainforests further east (Cameron 1984, Melick 1988), but they represent the most southerly extension of the east Australian warm temperate rainforest elements, with the excep-

tion of *Acmena smithii* which is present amongst cool temperate elements at Wilsons Promontory (Ashton & Frankenberg 1976). Moreover, the occurrence of *Brachychiton populneus* on the drier slopes at the Mitchell River is disjunct from its usual distribution in inland New South Wales and southern Queensland (Beadle 1981).

Many of the Gippsland rainforest communities have been subjected to fire, allowing the penetration of sclerophyll species, sometimes as emergents. Fossil evidence suggests that these small patches of rainforest represent the last vestiges of what were much more extensive warm temperate rainforests throughout eastern Victoria in the mid-Tertiary (Duigan 1951, 1965). The extent of the warm temperate rainforests is thought to have been reduced by fluctuations in climate together with increased fire frequencies (Ashton & Frankenberg 1976, Walker & Singh 1981). Contemporary rainforest distribution in Gippsland is likely to be regulated by moisture availability, disturbance and soil factors (Land Conservation Council 1985).

Although broad scale floristic surveys of the Gippsland region have been carried out previously (Gullan et al. 1981, Forbes et al. 1982), the present paper examines in detail the heterogeneous vegetation within a section of the Mitchell River National Park to determine the relative importance of topography, climate, distur-

bance and edaphic factors in the occurrence of rainforest and adjacent sclerophyll communities.

THE STUDY AREA

The survey covered an area of 143 hectares in the Mitchell River National Park (latitude 37°42'S, longitude 147°22'E), Victoria, some 220 km east of Melbourne (Fig. 1). The limits were determined by the boundaries of the former Glenaladale National Park, which was included within the new Mitchell River National Park in 1987. The area is noted for its rugged topography, including steep sandstone cliffs and limestone formations, and the presence of isolated warm temperate rainforest patches in sheltered sites amid sclerophyll vegetation.

Climate. The climate of the area is generally mild and, although at the southern fringe of the highlands, is tempered by the proximity to the coast 30 km to the south. At Glenaladale North (5 km south) the annual rainfall is 730 mm with a uniform seasonal distribution. The coefficient of variation is relatively high (27.7%) and extremes have led to prolonged droughts, as in 1965, 1972 and 1982 when the annual rainfalls were as low as 340 mm, or to severe floods, as in 1952, 1971 and 1978 (Ashton & Frankenberg 1976, and Bureau of Meteorology records) when annual rainfalls reached 1200 mm.

The mean annual temperatures at Bairnsdale (25 km south-west) range from 8.7°C to 19.9°C. At Glenaladale the range is likely to be

somewhat greater, and although frosts occur, they are not severe. Winds are predominantly from NW to SE with a strong SE component derived from east coast cyclones or from summer sea breezes. In winter, NW winds descending from the highlands result in milder conditions than at other sites in southern Victoria (Linforth 1969). The steep valleys and gorges in the park provide sheltered sites for vegetation in the area.

Physiography and geology. The physiography is dominated by the gorge of the Mitchell River which, following uplift in late Tertiary times (Easton 1938), has incised its bed 140 m into a low featureless plateau 170–200 m above sea level. Its tributaries in this area, Woolshed and Bull Creeks, have cut narrow rocky gorges for some distance from the Mitchell River. Instability of the rock faces has produced large-scale slumping and talus slopes, which have modified the form of the valleys. The increased meanders of the Mitchell River, in part due to the land slumps, have resulted in great variation in erosion and deposition. Deep scour holes alternate with shallow boulder areas and, where the velocity of the stream diminishes, point bars of sand have built up against major boulders. Geologically the region is part of the Avon River sequence of Late Devonian red-brown sandstones interbedded with soft shales and conglomerates (Easton 1938). Calcareous bands have been exposed along both the Mitchell River and the upper reaches of Bull Creek, but are most graphically displayed in the formation of the "Den of Nargun" on Woolshed Creek. This large cavern is the product of differential erosion, where intermittent stream action has undercut a hard calcareous bar by eroding away the underlying soft shale. Calcium carbonate leached from the sandstone has accumulated as stalactites and stalagmites in the Den.

Soils. Soils in the area are generally podzolic with sandy to sandy loam topsoils over yellow to reddish loam or clay loam subsoils. The depth of soils is highly variable and, being related to topography, is very shallow on upper slopes and plateau edges and relatively deep on lower slopes. On talus slopes soils are intermittently developed on small areas of calcareous rock bands and soils are brown loams to sandy loams, but in some places seepages occur on steep valley sides precipitating limestone shawls. On steeper slopes such lithological effects in soils are blurred by soil creep.

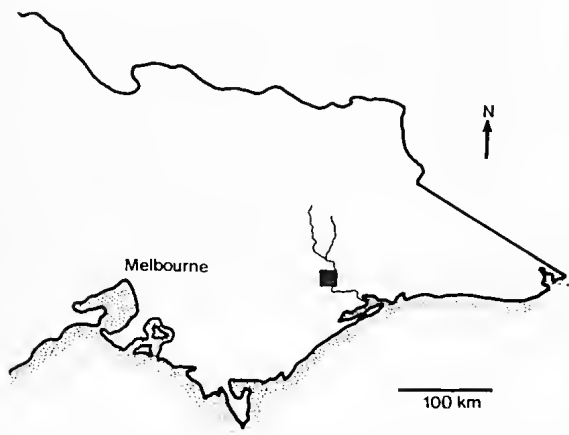


Fig. 1. Location of the Mitchell River National Park in Victoria.

In the valley floors soils are highly variable depending upon the nature of the parent material. Composition of the river and creek beds ranges from fine alluvial silts and clays to sands or skeletal layers of rocks and rubble from landslides; consequently some areas show a high content of organic matter while others are almost pure sand.

Land use and fire history. Aboriginal hunter-gathers lived in the region before Europeans colonized the area following the arrival of graziers in the 1840s (Land Conservation Council 1985). Accessible sclerophyll and grassy forest was cleared for improved pasture to support sheep and cattle grazing. Much land on poor soils has been abandoned and allowed to revert to shrubland, particularly in times of economic hardship.

As in most parts of Australia, the Glenaladale region has a long history of fire. Numerous fires have occurred this century, and in the most recent catastrophic fire in February 1965 extensive areas of the park were burnt. The fire passed over Woolshed Creek as a crown fire leaving the gully relatively undamaged; thus the rainforest of this gully epitomises the classic fireshadow (see Fig. 5A). A. W. Howitt, who in 1876 was the first European to visit this region, also noted this effect, commenting on "the cool moist atmosphere in the gorges while the bushfires rage overhead" (Howitt 1904). However, there is some evidence of spot firing and damage to trees due to flaming debris and rocks rolling down into the gully from the burning slopes above (Frankenberg 1965, Waller 1965).

The rainforest in Bull Creek was less fortunate as a south-westerly change blew the fire directly up the lower section of the creek, burning the vegetation in the gully and severely damaging it. The rainforest higher up the creek, however, was protected due to the changed direction of the valley and remained untouched (Waller 1965).

METHODS

Recording of vegetation. Vegetation was assessed in 1985 on the Braun Blanquet cover scale in 8 × 4 m quadrats, a size shown by minimal area quadrats to contain more than 85% of the species within a distinct community type. A total of 260 quadrats were surveyed as closely as practicable on a 75 m grid pattern, with some concentration on sites showing obvious topographic or floristic differences.

Where possible, all plant species were identi-

fied and recorded on site. Material that required further examination was collected and identified at Melbourne University and the National Herbarium of Victoria. Unless stated otherwise, nomenclature for vascular plant species follows Forbes & Ross (1988), for bryophytes Scott et al. (1976), and for lichens Filsen & Rodgers (1979). Nomenclature for vegetation in the study area is difficult due to the unusual plant associations, and so descriptive names have been used; e.g. damp sclerophyll (*sensu* Gullan et al. 1981). Where possible the structural classifications follow Specht (1970), but the term rainforest is employed in preference to closed forest due to the distinctly different species compositions of these communities.

Vegetation analysis. The floristic data (presence-absence) were assessed using both classificatory and ordination programs in the CSIRO TAXON library (Ross et al. 1983). The program MACINF (an update of MULTBET; Lance & Williams 1967) provided an hierarchical, polythetic-agglomerative classification. MACINF measures the dissimilarity of individual quadrats by the Shannon-type information statistic, and the fusion of these individuals into groups is based on a centroid sorting strategy. The diagnostic program GCOM (an update of GROUPER; Lance et al. 1968) was also used to identify the contribution of each species to the groupings at each level of the hierarchy. Initially a twenty group level was arbitrarily selected but the dendrogram was subjectively terminated at the six group level as further subdivisions were considered to be either minor variants or not meaningful. To complement the classification, the group centroids of the dissimilarity matrices produced by MACINF were ordinated by principal coordinate analysis (Gower 1966) using the program PCOA. To display the ordination of group centroids the three dimensional pattern was shown by using the minimum spanning ordination (MSO) technique of Gillison (1978). This technique displays the pattern of group centroids along the third axis in terms of a series of circles of graded size, with the largest and smallest circles representing the two groups which are farthest apart on the axis.

Insolation and moisture. The potential insolation at each site was determined from slope and aspect data obtained at each quadrat using the relationship given by Clifford (1951) for latitude 38°S. These values were corrected for any shading affecting the insolation due to the surround-

ing topography; the degrees of shading were determined using a contour map constructed from stereoscopic photographs.

At the end of the drought of 1983, the dawn water potentials of plant samples collected from various heights on the slope of the Woolshed Creek gully were measured in the field. Samples were stored in airtight plastic bags and water potentials were measured on a pressure bomb within 30 minutes of collection. During this drought the average visible crown damage to major species was visually estimated for the major species in the Woolshed Creek area. Fifteen individuals of each species were recorded and the average results tabulated.

Soil sampling and analysis. Surface soil samples (from 0–0.1 m deep) were collected at each quadrat site. Soil pH was measured on air-dried soil (<10 mm) by glass electrode in a soil-water slurry having a weight : volume ratio of 1 : 5. Particle size analysis was performed by the pipette and sieve method (Coventry & Fett 1979). Soil textures were categorized according to Leeper (1964) and soil colours were determined using a Munsell soil colour chart.

Prior to chemical analyses, samples were air-dried and sifted (<2 mm). Acid soluble and "adsorbed" phosphorus was extracted from soils by shaking samples in 0.1 N HCl and 0.03 N NH_4F for 40 seconds, as described for the Bray and Kurtz No. 2 phosphorus extraction (Jackson 1958). Phosphorus levels were then measured colorimetrically on a Technicon auto analyser. Exchangeable calcium was determined on air-dried soil (<2 mm) by ammonium saturation using 1 mol/L ammonium acetate at pH 7.0. Calcium levels within each leachate were analysed by atomic absorption spectrophotometry. Because the analysis of calcium by this method is subject to interference by anions, lanthanum (3000 ppm La in 0.8 N H_2SO_4) was added to each digest, to give a concentration of at least 1500 ppm La within each sample; this suppressed any interference by anions in the analysis.

RESULTS AND DISCUSSION

Environmental parameters

Insolation. The potential insolation over the area shows a wide range from 250–775 $\text{kJ}/\text{cm}^2/\text{yr}$ on the north and south facing slopes respectively of Woolshed Creek. There is only minor variation on the plateau areas, from about 630–700 $\text{kJ}/\text{cm}^2/\text{yr}$. These data suggest that moisture relations will be profoundly affected in sites where topography is complex.

Moisture. There was a progressive decrease in the relative water potentials of plants with increasing distance up the side of the gully at Woolshed Creek (Table 1), indicating the presence of a soil moisture gradient. Of the tree species present at Woolshed Creek, the greatest drought damage to foliage was observed in *Rapanea howittiana* and *Tristaniopsis laurina* (Table 2).

Soil. The results of the soil survey indicate that most of the area is covered with a top soil of sandy loam texture. Significant areas adjacent to Woolshed and Bull Creeks support sandy loams, and probably reflect the presence of shaly parent material. Some of the smaller areas of sands along parts of the stream courses appear to be related to depositional features.

The pH of surface soils shows considerable variation from acid (pH 4.2) to near neutral (pH 7.1) (Table 3). A large proportion of the area has soils with pH values from 5.0 to 5.9 but there are small areas, particularly in the upstream section of Woolshed Creek, where the pH is low (4.2–4.9). Neutral to slightly acid soils almost certainly reflect the proximity of calcareous beds, either *in situ* or upslope, and this is illustrated by

Species	Dawn water potential (MPa)		
	Gully floor	Mid slope	Top of slope
<i>Acmena smithii</i>	-1.13	-1.95	-2.22
<i>Pellaea falcata</i>	-0.38	-0.52	-0.58
<i>Pittosporum undulatum</i>	—	-1.76	-2.32

Table 1. Dawn water potentials of plants in the field on the northern aspect of the Woolshed Creek gully in February 1983.

Species	% of foliage showing drought damage
<i>Acacia mearnsii</i>	12.5
<i>Acmena smithii</i>	17.0
<i>Acrornychia oblongifolia</i>	9.5
<i>Kunzea ericoides</i>	6.0
<i>Pittosporum undulatum</i>	9.5
<i>Rapanea howittiana</i>	35.5
<i>Tristaniopsis laurina</i>	29.5

Table 2. Estimated average drought damage to the crowns of mature trees in the Woolshed Creek gully in February 1983. Each value represents the average of ten observations.

Environmental factor	Community type					
	A1	A2	B1	B2	C1	C2
Edaphic factors:						
pH	6.03 (4.8–6.7)	5.87 (4.2–7.4)	5.98 (4.8–6.3)	5.31 (4.3–6.4)	5.83 (4.8–7.1)	5.41 (4.7–6.8)
Acid extractable phosphorus (ppm)	49.4 (9.1–169.2)	32.8 (4.5–88.7)	31.5 (12.1–83.3)	46.3 (14.3–71.3)	21.5 (6.2–47.2)	24.0 (7.1–70.1)
Exchangeable calcium (ppm)	1180 (408–2101)	865 (322–1230)	1008 (475–1240)	587 (296–1138)	712 (420–1210)	602 (312–870)
Site insolation (kJ/cm ² /yr)	359.0 (250–660)	594.6 (388–750)	572.8 (390–670)	556.1 (410–685)	666.5 (452–760)	685.3 (510–775)

Table 3. Average values of environmental factors for community types. Figures in parentheses represent the range of values.

Environmental factors	Community types						Total No. sites for each factor
	A1 (27 sites)	A2 (30 sites)	B1 (28 sites)	B2 (29 sites)	C1 (61 sites)	C2 (85 sites)	
Soil pH	p < 0.05*	p < 0.9	p < 0.05*	p < 0.5	p < 0.05*	p < 0.01*	
(4.0–4.9)	1.00	1.16	0.20	1.60	0.27	1.37	47
(5.0–5.9)	0.63	0.94	0.93	0.88	1.11	1.16	152
(6.0–7.0)	2.00	1.00	1.71	0.86	1.26	0.30	61
Soil texture	p < 0.05*	p < 0.01*	p < 0.9	p < 0.7	p < 0.05*	p < 0.5	
(sand-loamy sand)	2.00	2.33	1.0	0.80	0.45	0.68	48
(sandy loam)	0.77	0.66	0.94	0.94	1.26	1.11	167
(s.clay loam–silty clay)	0.80	0.66	1.2	1.40	0.73	0.93	45
Acid extractable phosphorus	p < 0.01*	p < 0.2	p < 0.1	p < 0.001*	p < 0.001*	p < 0.1	
(0–25 ppm)	0.60	0.75	0.73	0.56	1.47	1.13	141
(25–50 ppm)	0.86	1.25	1.38	0.88	0.69	1.13	71
(> 50 ppm)	2.40	1.16	1.80	2.60	0.00	0.50	48
Exchangeable calcium	p < 0.05*	p < 0.2	p < 0.01*	p < 0.8	p < 0.7	p < 0.001*	
(0–499 ppm)	0.20	0.50	0.20	0.80	1.00	1.73	46
(500–1000 ppm)	0.94	1.05	0.89	1.11	0.92	1.09	163
(> 1000 ppm)	2.00	1.60	2.20	0.83	1.25	0.00	48
Site insolation	p < 0.001*	p < 0.2	p < 0.01*	p < 0.5	p < 0.01*	p < 0.01*	
(< 550 kJ/yr)	4.00	1.17	1.60	1.40	0.09	0.33	48
(550–650 kJ/yr)	0.36	1.33	1.50	0.83	1.15	0.89	109
(> 650 kJ/yr)	0.27	0.58	0.18	0.91	1.25	1.41	103

p = probability that the deviation is due to chance

*denotes statistically significant deviation from expected values at or above the 95% level.

Table 4. Chi-square analysis of environmental factors within each vegetation group and the ratios of observed value/expected value for the selected ranges of each factor.

the correlation of relatively alkaline soils with significantly higher exchangeable calcium levels (Table 4). Such soils are found along the lower section of Woolshed Creek, the northern plateau and seepage areas above the Mitchell River.

The values of acid (Bray-Kurtz) extractable phosphorus are likely to reflect not only the parent material and weathering processes, but also the degree and quality of litter cycling (Attiwill & Leeper 1987). The acid extractable phosphorus contents of the majority of soils in the area lay between 10 and 60 ppm, these being average levels for Australian soils (Beadle 1954, 1962). However, large areas of soils with low phosphorus levels (<20 ppm) occur on the plateaux under dry sclerophyll forest in the southern and northern parts of the park. Isolated pockets of soils with higher levels of phosphorus (60–170 ppm) occur along Woolshed and Bull Creeks. High phosphorus levels do not appear to have any consistent correlation with other soil properties (Table 4) but are probably due to increased nutrient cycling from the rainforest and from wet vegetation, as well as to the movement of soil and debris down the slopes of the gullies. However, the sand deposits in the creek beds under rainforest are very nutrient-poor, with available phosphorus levels of less than 10 ppm. Although sandy soils under the rainforest are very low in extractable phosphorus, the rate of release of nutrients from litter fall may be more significant than a static value at any one time.

Description of vegetation

From the numerical analyses of floristic data three supergroups, each representing community types, were delineated: A (rainforest communities), B (damp sclerophyll communities), and C (dry sclerophyll communities). Each of the three supergroups include two subordinate groups: A1, A2; B1, B2; and C1, C2. These subordinate groups represent the six community types recognized in this study.

The dendrogram illustrating the hierarchical relationship, and the ordination plot showing the relative similarity of the six community groups, are shown in Figs 2 and 3 respectively. The six major community types recognized are described below and their locations within the study site are mapped in Fig. 4. The frequencies of species within each of these community types are listed in Appendix 1.

Supergroup A. Rainforest communities

These communities were clearly delineated floristically in the classification and ordination by

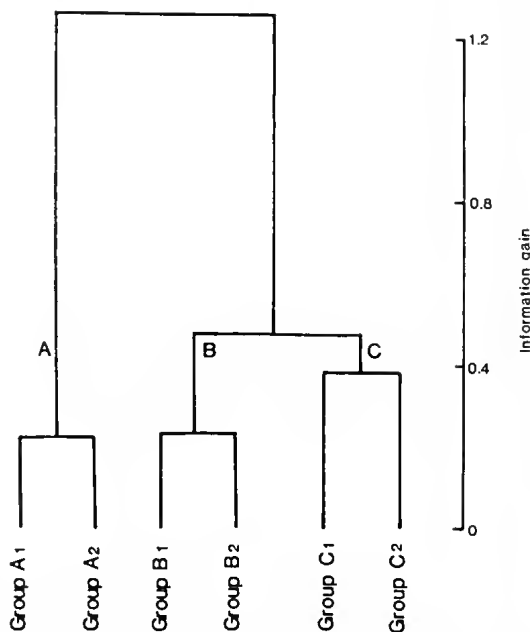


Fig. 2. Dendrogram showing the hierarchical classification (MACINF) of 260 quadrats above the 6 group level of the community types.

57 quadrats. Supergroup A was divided into two groups, one being typical closed forest along Woolshed Creek and upper Bull Creek (group A1), the other being more open and disturbed as a result of the 1965 fire along the lower reaches of Bull Creek and the banks of the Mitchell River (group A2).

Undisturbed rainforest (group A1, 27 quadrats). A closed canopy (>85% cover) up to 35 m tall and composed of *Aemena smithii*, *Pittosporum undulatum*, *Acrornychia oblongifolia* and *Tristaniaopsis laurina* dominates this community. Thin wiry and slender woody lianes (*sensu* Webb 1978), such as *Morinda jasminoides*, *Smilax australis*, *Eustreplus latifolius*, *Marsdenia rostrata* and *Pandorea pandorana* are abundant. A sparse understorey (average 6% cover) of the shrubs *Olearia argophylla*, *O. lirata*, *Hymenanthera dentata* and *Coprosma quadrifida* is present. The rainforest supports a wide variety of ferns, including *Pellaea falcata*, *Adiantum aethiopicum*, *Asplenium flabellifolium*, *Doodia aspera*, *Polystichum proliferum*, *P. formosum*, *Microsorium diversifolium* and the tree ferns *Dicksonia antarctica* and *Cyathea australis*. The mosses *Breutelia affinis* and *Thuidium laevisculum* are also very prominent in the ground stratum, while *Weymouthia cochlearifolia* is a

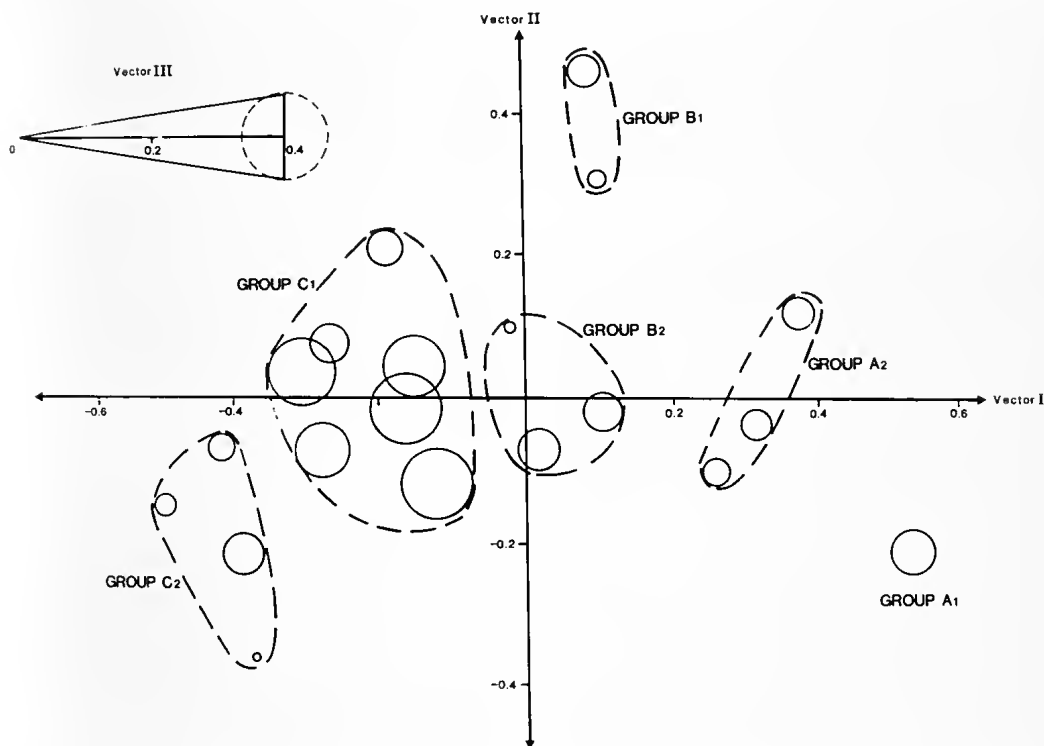


Fig. 3. PCA ordination plot illustrating the relationship between the 20 group centroids initially delineated by the MACINF program from which the 6 major community groups were selected.

very common epiphyte. This unburnt forest best conforms to closed forest in respect to Specht (1970) and microphyll fern forest according to Webb's (1968) general physiognomic-structural rainforest classification. The species composition is similar to, though somewhat more attenuated than, the warm temperate rainforest described by Forbes et al. (1982) in East Gippsland.

Disturbed rainforest (group A2, 30 quadrats).

Burnt forest is more open and contains fewer lianes and less variety of ferns than the undisturbed rainforest, supporting instead a denser sclerophyllous understorey and a greater number of herbs and graminoids. *Tristaniaopsis laurina* and to a lesser extent *Acmena smithii* form a canopy with an average cover of 40%; i.e. at the present time this community is an open forest but it seems likely to regenerate a rainforest canopy. The understorey (approximately 40% cover) consists mainly of *Pomaderris aspera* and *Baeckea virgata* in conjunction with *Kunzea eri-*

coides. In the ground stratum *Dichondra repens*, *Geranium solanderi*, *Hydrocotyle hirta* and *Oxalis corniculata* together with the grasses *Microlaena stipoides* and *Oplismenus aemulus* are prevalent. Although the variety of ferns found in the undisturbed rainforest is lacking, *Pellaea falcata*, *Adiantum aethiopicum* and *Asplenium flabellifolium* are abundant. The vines within this community are poorly developed and generally may be classified as thin wiry lianes (*sensu* Webb 1978). This community may be regarded as a simplified version of Webb's (1968) microphyll fern forest.

Supergroup B. Damp sclerophyll communities

These communities have suffered variable degrees of fire disturbance and the overstoreys are dominated by eucalypts. The ordination clearly delineates these groups and suggests an important habitat control associated with the presence of ferns and typical wet sclerophyll species. Floristically these communities are quite bizarre, having dry and wet sclerophyll together

with occasional rainforest species, and thus categorisation is difficult. In terms of the communities described in central Gippsland by Gullan et al. (1981), these groups are probably best regarded as damp sclerophyll communities, although rainforest species are not characteristic for these vegetation types.

Damp sclerophyll woodland (group B1, 28 quadrats). In this unusual community a sparse canopy (20% cover) of *Eucalyptus globulus* ssp. *bicostata*, *E. polyanthemus* and *E. melliodora*, up to 30 m tall, is present over a dense understorey (75% cover) of *Acacia mearnsii* and *Pomaderris aspera* scrub from 8–18 m high. Dense lianes of *Pandorea pandorana* and *Clematis glycinoides* are found throughout the understorey. A well developed ground stratum contains shade tolerant herbs such as *Microlaena stipoides*, *Dichondra repens*, *Goodenia ovata*, *Oxalis corniculata* and *Hydrocotyle hirta*. The sedge *Lepidosperma laterale* and the fern *Pellaea falcata* are abundant. This community occurs on the relatively cool south-easterly slope above the Mitchell River, and the presence of burnt stumps in some places and occasional coppice of regenerating *Acmena smithii* suggest that this site once supported a form of wet sclerophyll forest with areas of hillside rainforest.

Layered tall open forest (group B2, 29 quadrats). This heterogeneous community occurs mainly along the southern aspects of the upper Woolshed Creek, with pockets on other relatively sheltered eastern aspects. *Eucalyptus globoides*, *E. polyanthemus* and *E. cypellocarpa* growing to over 30 m high are present as an open overstorey (average crown cover of 37%) over a reasonably thick scrub (54% cover) of *Kunzea ericoides*, *Acacia mearnsii* and *Baeckea virgata* scrub (in riparian areas) from 6–12 m high. Some rainforest elements occur, a few individuals of *Tristaniaopsis laurina*, *Pittosporum undulatum* and *Rapanea howittiana* being present in quadrats near the rainforest boundary. The ground stratum is diverse, including mosses and ferns, of which *Adiantum aethiopicum* and *Cheilanthes tenuifolia* are the most abundant. The shade tolerant herbs *Microlaena stipoides*, *Hydrocotyle hirta*, *Dichondra repens*, *Veronica plebeia* and *Goodenia ovata* are also present in the field layer, together with ubiquitous *Lepidosperma laterale*.

Supergroup C. Dry sclerophyll communities

These communities are classified by their floristic

association and show a variable range of structures. These complex mosaics are dominated by *Eucalyptus globoides* with variable mixtures of *E. polyanthemus*, *E. melliodora* and *Brachychiton populneus*. The understoreys are commonly dominated by *Acacia mearnsii* and *Kunzea ericoides*, while a variety of sedges, grasses, herbs and ferns may be present in the ground stratum.

The floristic groupings of the computer classification show a continuum ranging from open forest with predominantly grassy understoreys of *Styphandra glauca* and *Lepidosperma laterale* (group C1) to woodlands with very dense scrubby understoreys of *Acacia mearnsii* and *Kunzea ericoides* (group C2).

Sclerophyll open forest (group C1, 61 quadrats). An open forest of *Eucalyptus globoides*, and to a lesser extent *E. polyanthemus*, is found in the north-west of the park on the cooler southern and eastern aspects, and in a small patch on the northern aspect of the ridge below Woolshed Creek. The average crown cover of the eucalypt overstorey is 60% and the mean height is about 26 m. The sparse ground stratum (33% cover) is dominated by the lily *Styphandra glauca*, together with the sedges *Gahnia radula* and *Lepidosperma laterale*. The presence of *G. radula*, which is an indicator of seasonal waterlogging (Clifford 1952), in the north-west of the site suggests this area is poorly drained; such a moist habitat would explain the common occurrence of the fern *Adiantum aethiopicum* in the ground flora in these areas. On the hotter ridge sites the dwarf sclerophyllous shrubs *Phyllanthus hirtellus*, *Pomax umbellata* and *Leucopogon ericoides* become prominent in the field layer. Although *Kunzea ericoides* is present in the understorey it is only patchy, having an average cover value of 27%.

Sclerophyll woodlands and scrub (group C2, 83 quadrats). This community, which occurs on gently sloping terrain from the vicinity of the creeks to the broad ridges, shows great structural variation, with patches of woodland (64.5% plots) with scrubby understorey amid dense scrubland (35.5% plots). Woodland up to 25 m in height is composed predominantly of *Eucalyptus globoides* with *E. polyanthemus* occurring occasionally. However, the community is overwhelmingly dominated by dense stands (78% cover) of *Kunzea ericoides* and *Acacia mearnsii* 4–15 m tall. The great dominance of the scrub has generally depleted the ground

layer, but shade tolerant herbs such as *Wahlenbergia quadrifida*, *Oplismenus aemulus* and *Microlaena stipoides* together with the fern *Cheilanthes tenuifolia* are sometimes present, and *Lepidosperma laterale* is represented in the gaps.

Factors affecting vegetation patterns

Topography and fire. The ordination of the group centroids by the PCOA program separates the community types along the three vectors (Fig. 3). The first vector carries 71% of the information, the second 20%, and the third 9%. Of these vectors only the first two are ecologically interpretable. Vector I, which is positively correlated with rainforest species (i.e. *Acmena smithii*, *Acronychia oblongifolia*) and negatively correlated with dry sclerophyll species (i.e. *Phyllanthus hirtellus*, *Pomax umbellata*), appears to reflect the relative exposure and moisture of each community (topographic effects). The position of the groups along vector I shows a continuum, with a transition from the dry sclerophyll communities (groups C2, C1) through to damp sclerophyll (groups B2, B1) to the undisturbed rainforest (group A1). This ecological interpretation of the ordination plot is

supported by the insolation data which show a progressive increase in site insolation for the community types listed above (Tables 3, 4). The position of groups along vector II is chiefly determined by a positive correlation for *Pomaderris aspera* and this effectively separates the damp fire-disturbed B1 community.

The relationship between the plant communities and topography also appears to be related to the fire susceptibility of the sites. Hotter and drier sites on the ridge tops and plateaux are generally more fire prone than those in the sheltered gorges and gullies, and this is reflected in the distribution of community types in the study area (Fig. 4). The fire protection afforded by the steep gorge walls and surrounding vegetation has created a humid microclimate that allows the survival of warm temperate rainforest (Fig. 5A, B). Damp sclerophyll scrub grows on the margins of the rainforest and on the cooler eastern-facing slope above the Mitchell River, but with increasing exposure on the upper slopes and ridges there is a sharp change to the drier sclerophyll forests and scrubs. The fire susceptibility implied by the topographic and insolation data is supported by direct observation of charcoal and fire damage in many of the sclerophyll communities.

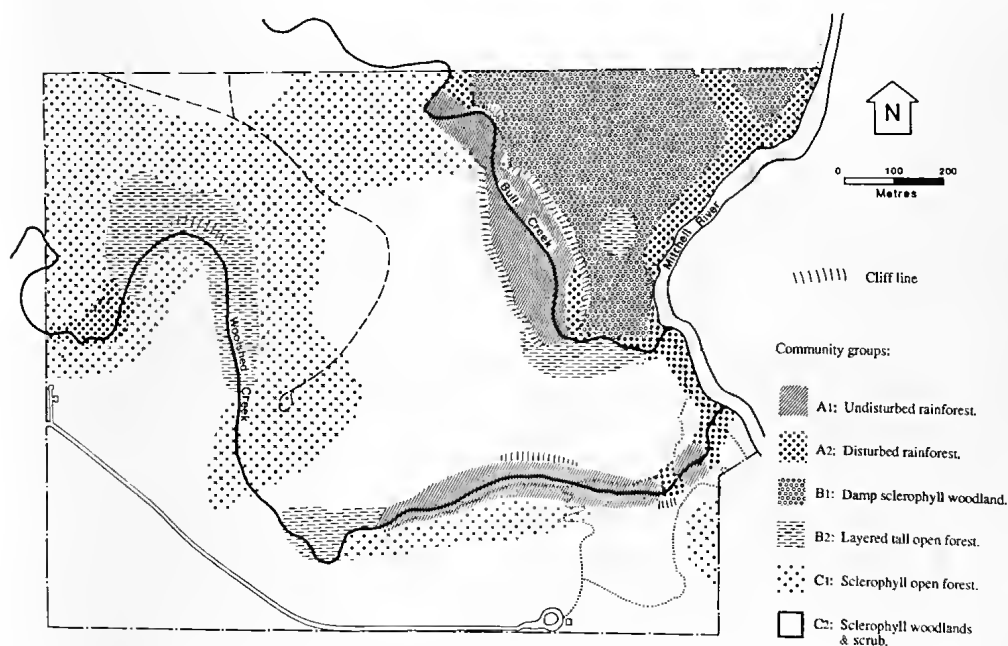


Fig. 4. Distribution of community types within the surveyed area bounded by the previous limits of Glenaladale National Park. Communities are delineated on the basis of the 260 quadrats surveyed in the area.

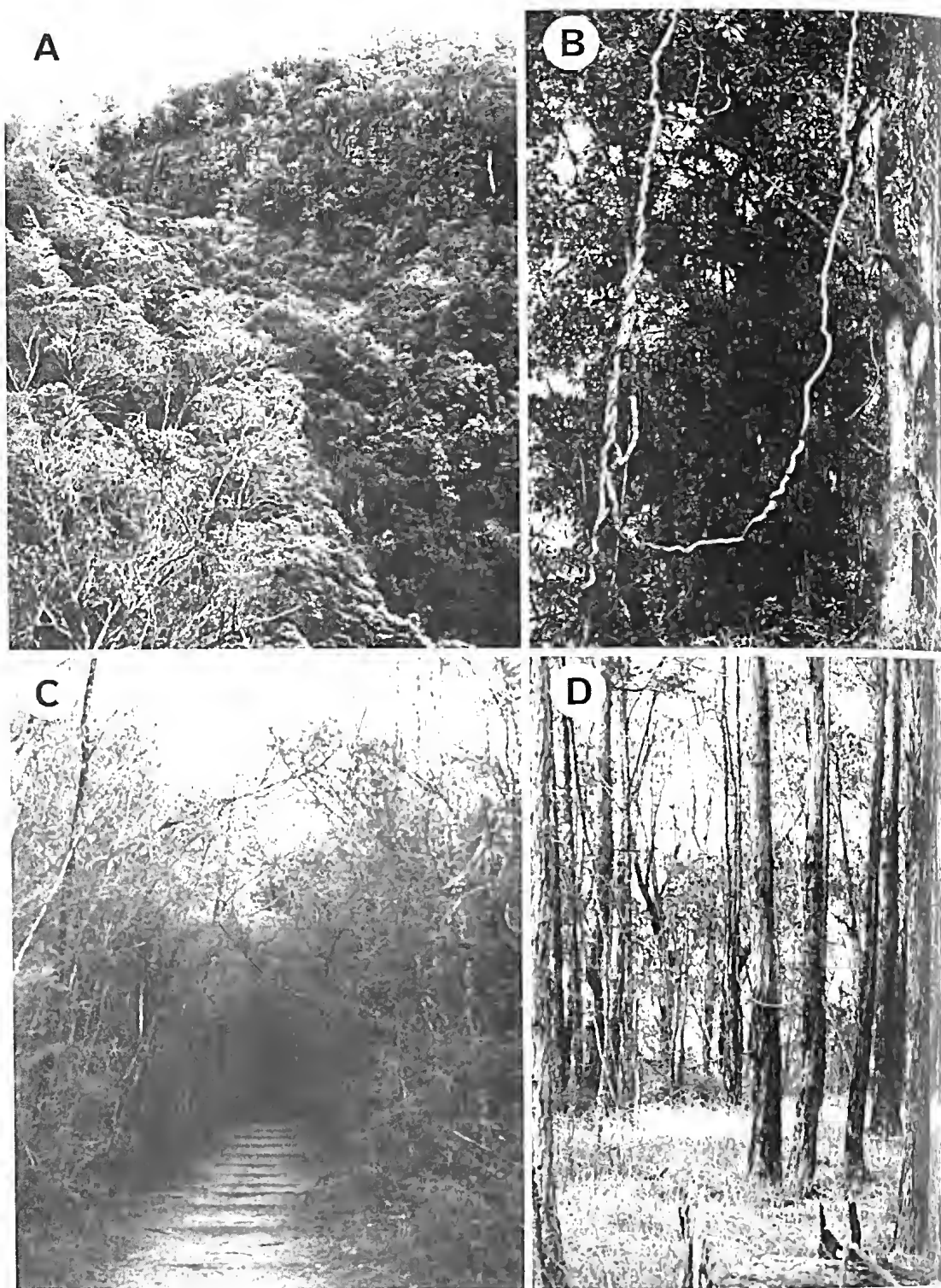


Fig. 5. A, the Woolshed Creek gully following the 1965 bushfire, illustrating the fireshadow effect protecting the rainforest community. B, warm temperate rainforest in the Woolshed Creek Gully. C, thick *Kunzea ericoides* and *Acacia mearnsii* scrub in an area previously cleared and burnt. D, sclerophyll open forest of *Eucalyptus globulus* over a graminoid-rich field layer.

The restriction of the rainforest to fire-sheltered sites is obvious at present, but observations at the study sites suggest that in the absence of fire the rainforest may spread from the sheltered gorges. The presence of the simplified rainforest communities (A2) in more exposed sites may indicate that the rainforest has the ability to expand to these areas. Similarly, the occurrence of rainforest seedlings in the damp sclerophyll vegetation suggests that these communities are being invaded by the rainforest.

Fire and clearing disturbances also appear to be important factors in determining the floristic patterns of the sclerophyll communities (Fig. 4). Fire has allowed the establishment of *Pomadouris aspera*, a seral species in the succession after fire (Cunningham & Cremer 1965), in the damp sclerophyll woodland (group B1). Furthermore, it is suggested that the occurrence of the dry sclerophyll scrub communities (group C2) on the flatter terrain in the south and on the broad central spur between Woolshed and Bull Creeks is, in part, the result of historical disturbance. These areas which were cleared, grazed and burnt (as evidenced by the presence of ring-barked trees, stumps and charcoal) have undergone prolonged secondary succession both before and after the 1965 bushfire. Clearing appears to have allowed the invasion of *Kunzea ericoides*. Moreover, the severe fire of 1965 has seemingly enabled the establishment of thick *Acacia mearnsii* scrub and enhanced the regeneration of *K. ericoides* (Fig. 5C). Similar behaviour of *K. ericoides* has been noted in New Zealand where this shrub is regarded as a seral species following fire and soil disturbance in closed forests and agricultural land (Payton et al. 1984, Mark et al. 1989, Partridge 1989).

In the open sclerophyll forest (group C1), where disturbance has been less severe, the ground stratum is generally dominated by graminoids, and gap phase shrubs are relatively rare (Fig. 5D). Similarly, on the lower slopes of the sclerophyll woodland communities where eucalypts have survived the fire and regenerated, thick *Acacia mearnsii* and *Kunzea ericoides* scrub is limited to small patches occurring in gaps formed by the collapse of larger trees. *Acacia mearnsii* in particular is commencing to senesce in the normal course of secondary succession following the 1965 fire; however, dying shrubs are creating gaps which are being colonized by seedlings of *K. ericoides* without the intervention of fire. Similarly, *K. ericoides* has established in gaps within the rainforest community created by endogenous disturbances.

Throughout the study site *Kunzea ericoides* appears to act as a persistent and aggressive colonizing species, consistent with observations by Judd (1990) in open forests in central Victoria and southern Gippsland.

Water availability. Site moisture plays an important role in the distribution of vegetation at the study site. The climate of the Mitchell River area is relatively dry with regard to the rainforest communities, the average annual rainfall (730 mm) being significantly less than the mean annual rainfall of 1004 mm for what Webb et al. (1984) have determined to be the average climatic region for microphyll vine-fern rainforest types. Moreover, rainfall at the Mitchell River site falls below the 750 mm annual rainfall limit which has been suggested as the lower threshold for the maintenance of rainforests in temperate zones (Beadle 1981, Webb & Tracey 1981). Certainly, the moisture gradient indicated by the relative water potentials of species across the Woolshed Creek gully seems to limit the extension of rainforest up the side of the gully, as even on the unburnt slopes the rainforest is restricted to the lower half of the gully. Observations in this area indicated that *Acmena smithii* plants higher on the slopes were killed during severe droughts in 1972 (D. H. Ashton pers. comm.). Moisture availability, rather than shelter, also seems to limit the distribution of *Tristanopsis laurina*, which appears to be drought intolerant, as this species is present in riparian situations, both in the sheltered gullies in the unburnt rainforest (group A1) and as a dominant species in the relatively exposed sites on the river where the rainforest has been disturbed by fire (group A2).

Similarly, moisture is an important factor for the presence of damp sclerophyll scrub and rainforest elements on the easterly slope above the Mitchell River. The concave profile of this slope implies that land slumping has occurred (Easton 1938), a phenomenon often associated with features of subterranean drainage (Strahler 1973). The possibility of drainage at this site would enhance the establishment of moist communities. This is supported by field observations which revealed a tendency for the base of this slope to be moist, even during summer, while elsewhere at the study site wet sclerophyll species were wilting. In contrast, the dry sclerophyll communities dominate the dry plateaux and ridge tops, where insolation is greater and water tables are likely to be much lower.

Edaphic factors. There is some correlation between the topsoils and the vegetation patterns, but it seems that the former are of secondary importance to topographic features. Although the undisturbed rainforest community (A1) occurs most commonly on less acidic soils (Table 2), this is probably a reflection of the fact that the protected gullies, to which the rainforest is restricted, are eroded through limestone bands. It seems unlikely, therefore, that soil factors *per se* are limiting the rainforest distribution, a view supported by the fact that the disturbed rainforest (A2), which occurs outside the deeply eroded gullies, is present on soils with a wide range of pH (Tables 3, 4). Similarly, the relatively high pH and exchangeable calcium levels of soils associated with the damp sclerophyll scrub (group B1) may be attributed to the apparent leaching of limestone on the eastern hillside, or to the fact that *Pomaderris aspera*, which is dominant in this community, is known to return high amounts of calcium to the soil (Ashton 1981). The varied surface soil characteristics within the dry sclerophyll communities further demonstrate the primary role of topography rather than edaphic factors in determining vegetation types at this site. Eucalypt open forest (group C1) showed a statistically significant correlation with less acidic soils (Table 4), due to a large tract of this community growing on relatively high pH soils in the northwestern corner of the study area, but this community type extended across to the adjacent more acidic soils on the central plateaux, with no discernible effect on the vegetation. The soils on the ridges and flats dominated by the scrubby eucalypt woodlands (group C2), however, were generally more acidic.

The general trend of higher phosphorus levels in soils associated with damp sclerophyll and rainforest communities than with dry sclerophyll communities was not unexpected. Again, however, the extractable phosphorus content may be a reflection of the type of vegetation cover rather than a factor limiting its distribution, since nutrient turnover is much more rapid in moist forests than in dry ones (Attiwill & Leeper 1987). Although the average extractable phosphorus levels of soils associated with the rainforest and damp sclerophyll communities were relatively high, it should be noted that the range of values was also high (Table 3), with isolated pockets of fertile soil amongst low phosphorus soils indicating localized enrichment. Such enrichment may result from landslips, flood accumulation of colloidal material, and

lyrebird activity to which these sites are susceptible. The heterogeneity of the moist forest soils within the study site is highlighted by the fact that, amid the generally high fertility rainforest soils, the floors of the gullies supporting riparian rainforest communities are composed of immature soils and nutrient-poor sands deposited during floods (Table 3). The predominance of *Tristaniopsis laurina* in the creek beds suggests that this may be the rainforest species that is best adapted to this environment, in which the intrinsic nutrient status of the sands is poor although the flux of nutrients through the system, following flooding, may be great (Melick 1990).

SUMMARY

The study area is topographically delineated by lithology and by gorges cut by streams. The relatively moist conditions and the shelter provided from wind and fire has permitted the survival of warm temperate rainforest in the gullies. Fire disturbance seems to have played a major role in the floristics of present communities by simplifying the burnt rainforest (A2) and allowing the establishment of damp sclerophyll communities (B1, B2). Fire also appears to have induced a massive germination of *Acacia mearnsii* seed and regeneration of *Kunzea ericoides* from seed and lignotuber. Woodland and scrub areas may be due in some places to shallow rocky soils and hot dry aspects but they also seem to reflect a past history of forest clearing. The combination of the above factors together with the mild climate and erratic rainfall of this region has led to many unusual plant associations and to heterogeneity within communities, making their classification difficult. This difficulty has been reflected in the surveys of Gippsland vegetation (Gullan et al. 1981, Forbes et al. 1982) in which descriptions of community types take the form of "common names", and which are not intended to form the basis for a formal nomenclature. Some of the community types delineated in the present paper are comparable to subcommunities identified in these earlier surveys but, owing to the broad scale of those surveys, such comparisons are not very specific.

The high pH levels and exchangeable calcium contents of surface soils throughout the park appear to reflect the distribution of limestone bands underlying the area. Soil characters show some correlation with vegetation distribution but these trends could be the result of vegetation

modifying the topsoil chemistry. The dramatic topography and history of disturbance in this area seem to be more important than soil differences in determining the distribution of vegetation.

Because of the importance of fire disturbance as a limiting environmental factor, the unburnt rainforest patches are best classified under the second of Webb & Tracey's (1981) types of rainforest refugia, as they are restricted to small, relatively dry and fireproof topographic niches. However, the disturbed rainforest along the river and shallow gullies can be construed as small, narrow gallery forests, falling under the third of Webb & Tracey's (1981) refugia classifications. Since many of the rainforest species occur at their climatic limits at the Mitchell River sites, the nature and frequency of disturbances play a particularly important role in determining the extent and floristic composition of rainforest communities in these areas.

The relative importance of the various ecological factors examined in this study are likely to apply to comparable mosaics of rainforest and sclerophyll forest occurring at the limits of distribution for rainforest types. Although soil chemical properties are involved in the delineation of rainforest and sclerophyll communities in Queensland and New South Wales (Beadle 1954, 1962, 1966, Webb 1968, 1969), the importance of edaphic factors is often diminished relative to climate, topography and disturbance history, particularly in areas under less than ideal conditions (i.e. higher latitudes) (Mount 1964, Tracey 1969, Webb 1969, Beadle 1981, Webb & Tracey 1981). Certainly, studies at some sites in East Gippsland (Melick 1988) indicate that natural disturbances and topography generally appear to be far more important than edaphic factors in determining the occurrence of rainforest and sclerophyll communities.

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APPENDIX 1

Details of the vegetation community types.

The percentage of sites in which each species occurred for each of the community types. Figures in parentheses represent percentage of sites where species cover exceeded 5%.

Species	A1	A2	Community Type		C1	C2
			B1	B2		
TREES						
<i>Acmena smithii</i>	94 (88)	39 (39)	8			
<i>Acronychia oblongifolia</i>	44 (25)	13 (4)				
<i>Brachychiton populneus</i>		4 (4)	4 (4)			2 (2)
<i>Eucalyptus cypellocarpa</i>			4 (4)	28 (24)		2 (2)
<i>Eucalyptus globoides</i>		13 (13)		55 (55)	98 (98)	55 (55)
<i>Eucalyptus globulus</i> ssp. <i>bicostata</i>			24 (20)			4 (4)
<i>Eucalyptus melliodora</i>			4 (4)	4 (4)	2 (2)	6 (6)
<i>Eucalyptus polyanthemus</i>		4 (4)	44 (44)	41 (41)	40 (40)	14 (14)
<i>Exocarpos cupressiformis</i>				4 (4)	3	2 (2)
<i>Pittosporum undulatum</i>	63 (56)	9 (4)		7 (3)	3 (3)	2
<i>Rapanea howittiana</i>	6	4 (4)	8	4		
<i>Tristanopsis laurina</i>	25 (19)	70 (65)	4 (4)	3 (3)		
SHRUBS						
<i>Acacia falciformis</i>					2	3 (2)
<i>Acacia inplexa</i>		4	16 (4)	7 (4)	3	1
<i>Acacia mearnsii</i>		17	100 (96)	41 (34)	40 (29)	93 (87)
<i>Baeckea virgata</i>		52 (35)	4 (4)	41 (32)	1	1
<i>Callistemon paludosus</i>		4				
<i>Cassinia longifolia</i>			28 (4)	28 (3)	76 (2)	18
<i>Cassinia trinerva</i>			12	4		2
<i>Coprosma quadrifida</i>	44	9	4	7		
<i>Correa lawrenciana</i>			4			
<i>Correa reflexa</i>			20	14	13 (2)	1
<i>Epacris impressa</i>				4 (4)		1
<i>Hakea eriantha</i>			12 (4)			
<i>Helichrysum dendroideum</i>		4	8	10	10	2
<i>Hibbertia obtusifolia</i>				4	10	11
<i>Hymenantliera dentata</i>	81	17		10	3 (1)	
<i>Indigofera australis</i>		9	4			1
<i>Kunzea ericoides</i>	6	39 (13)	24 (16)	90 (59)	64 (46)	96 (89)
<i>Leucopogon ericoides</i>		4	4	21	28	36
<i>Lomatia myricoides</i>		4				
<i>Olearia argophylla</i>	31 (25)	9	4	4	3	1
<i>Olearia lirata</i>	25 (6)	13	24 (4)	10 (7)		
<i>Olearia rugosa</i>		4	4			
<i>Phyllanthus hirtellus</i>				7	61 (1)	49 (2)
<i>Pimelea axiflora</i>	6	4	48	3		2
<i>Pomaderris aspera</i>		52 (43)	84 (76)	7 (3)		10
<i>Prostanthera rotundifolia</i>				17 (3)		
LIANES						
<i>Clematis glycinoides</i>	50	57 (9)	44	28	3	5
<i>Eustrephus latifolius</i>	56	39	8	7	2	1
<i>Geitonoplesium cymosum</i>	38	13				2
<i>Glycine clandestina</i>				21	1	21
<i>Kennedia rubicunda</i>	6			7		7
<i>Marsdenia rostrata</i>	88 (50)	48 (4)	24 (4)	3	1	2
<i>Morinda jasmuinoides</i>	56 (6)	30	4			
<i>Pandorea pandorana</i>	6	43	88 (8)	31	17	5 (1)
<i>Smilax australis</i>	75 (19)	39 (4)				

Species	A1	A2	Community Type		C1	C2
			B1	B2		
GRAMINOIDS						
<i>Agrostis</i> spp.		4	20 (4)	10 (4)	10	3
<i>Danthonia</i> spp.		22 (4)	24	35	43	48 (2)
<i>Echinopogon ovatus</i>				7	25	12
<i>Entolasia marginata</i>	44	35				
<i>Gahnia melanocarpa</i>		4	16 (4)	24		17
<i>Gahnia radula</i>		35 (13)		17 (3)	45 (3)	20 (2)
<i>Juncus planifolius</i>			4			
<i>Lepidosperma laterale</i>	13	26 (9)	96 (40)	69 (31)	77 (10)	51 (12)
<i>Lomandra longifolia</i>	13	22			29 (2)	1
<i>Microlaena stipoides</i>	13	65 (18)	82 (12)	55 (3)	54 (1)	75 (20)
<i>Oplismenus aemulus</i>	13	74 (9)	52	24	17	19
<i>Poa</i> spp.		9	4 (4)	4	11	
<i>Stipa</i> spp.			4		1	7 (5)
<i>Stypandra glauca</i>				3	90 (30)	6 (3)
<i>Themeda australis</i>				4		5 (1)
<i>Wahlenbergia quadrifida</i>		9	36	55	57	51 (1)
<i>Xanthorrhoea minor</i>				4	22 (6)	19 (2)
FORBS						
<i>Acianthus exsertus</i>		4			2	
<i>Australina muelleri</i>	69 (6)	9		3		
<i>Centaureium minus</i>		4		10	2	8
<i>Chiloglottis reflexa</i>		4				
<i>Conyza</i> spp.	6		8	4		
<i>Cynoglossum latifolium</i>	6	22				
<i>Dichondra repens</i>		65 (13)	84	69 (7)	13	52
<i>Galium</i> spp.		17		41	25	18
<i>Geranium solanderi</i>	31	52 (4)	8	17	2	13
<i>Gnaphalium involucratum</i>		9		10 (4)	5	1
<i>Gnaphalium japonicum</i>		22 (4)	24	35	33	14
<i>Goodenia ovata</i>	6	13 (4)	48 (32)	31 (14)	4	4
<i>Hydrocotyle hirta</i>	6	35	56 (4)	72 (10)	32	33
<i>Hydrocotyle laxiflora</i>		4				
<i>Hypericum gramineum</i>	6	9	20	4	3	13
<i>Hypochoeris radicata</i>	19	26	36	14	3	16
<i>Lagenophora gracilis</i>		9	8	4	6	4
<i>Luzula campestris</i>			4	4	2	4
<i>Onopordum acanthium</i>		4 (4)	8			2
<i>Opercularia ovata</i>			24	35	45	26 (1)
<i>Oxalis corniculata</i>		48	56 (4)	21	8	8
<i>Plantago debilis</i>	6	22	8	21		2
<i>Plectranthus parviflorus</i>	19	4	24		5 (2)	5
<i>Polygonum</i> spp.		9				1
<i>Pomax umbellata</i>					22 (1)	1
<i>Pterostylis concinna</i>					16 (1)	
<i>Rhagodia nutans</i>		4	4			
<i>Rubus fruticosus</i>	56	22	4			
<i>Rumex acetosella</i>	6	13	4	7		
<i>Senecio linearifolius</i>		22	20	3		4
<i>Senecio minimus</i>	13		20	17	2	4
<i>Sigesbeckia orientalis</i>	13	4				2
<i>Solanum nigrum</i>						2
<i>Solanum prinophyllum</i>		13	24	14	5	10
<i>Stellaria flaccida</i>	63	30	2	7		
<i>Taraxacum officinale</i>	6	4	8		3	6
<i>Thysanotus patersonii</i>						2
<i>Tradescantia fluminensis</i>	6	17		4		

Species	A1	A2	Community Type		C1	C2
			B1	B2		
<i>Trifolium repens</i>		4				4
<i>Urtica incisa</i>	50 (13)	22 (4)	8	10		1
<i>Veronica plebeia</i>			12	38	16	14
<i>Viola betonicifolia</i>		13		7	2	8
<i>Viola hederacea</i>		13	20	10 (4)		5
FERNS						
<i>Adiantum aethiopicum</i>	25	52 (4)		55 (10)	20	1
<i>Asplenium flabellifolium</i>	44 (6)	52 (4)	8	24		
<i>Blechnum nudum</i>	19	17 (4)	4			
<i>Cheilanthes tenuifolia</i>	13	35	36	79 (3)	68	36
<i>Cyathea australis</i>	6					
<i>Dicksonia antarctica</i>	31 (13)					
<i>Doodia aspera</i>	50 (19)	26 (4)		3		
<i>Hymenophyllum</i> spp.	13					
<i>Microsorium diversifolium</i>	56 (13)					
<i>Microsorium scandens</i>	13					
<i>Pellaea falcata</i>	75 (13)	91 (26)	48 (4)	17 (3)		
<i>Pleurosorus rutilifolius</i>					3	1
<i>Polystichum formosum</i>	56 (19)	4	16		2 (2)	
<i>Polystichum proliferum</i>	63 (25)	4				
<i>Pteridium esculentum</i>	19	13		3	14 (2)	
<i>Pyrrosia rupestris</i>	44					
BRYOPHYTES						
<i>Breutelia affinis</i>	56 (19)	30 (4)	8			
<i>Campylopus</i> spp.	25 (6)	39	36	62 (10)	48	61
<i>Cyathophorum bulbosum</i>	19	4		3		1
<i>Dawsonia polytrichoides</i>	6			10		
<i>Thuidium laeviusculum</i>	100 (75)	70 (9)	28	55 (3)	13	23
<i>Weymouthia cochlearifolia</i>	69 (44)	4				
LICHENS						
<i>Cladia aggregata</i>	13	9	4	31 (3)	13	15
<i>Heterodea muelleri</i>	50 (6)	48	36	62 (3)	67 (10)	47 (1)
<i>Pseudocyphellaria glabra</i>	38	13		10	3	1
<i>Usnea</i> spp.	31	13	32	35	29	33
AVERAGE ROCK COVER (%)	80.2	16.8	6.4	14.0	20.1	6.0

ASPECTS OF THE LIFE HISTORY OF THE TWO-SPINED BLACKFISH *GADOPSIS BISPINOSUS* IN KING PARROT CREEK, VICTORIA

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The population of the two-spined blackfish, *Gadopsis bispinosus*, in King Parrot Creek, Victoria consisted mainly of individuals with total lengths from 30 to 190 mm. Individuals longer than 210 mm comprised less than 2 % of the total sample of 1054 fish. Juvenile recruitment occurred in summer. Length-weight relationships indicate that females are slightly heavier than males. The spawning season, as inferred from ovarian development, was from October to December when water temperatures increased rapidly from the winter minimum. The seasonal nature of ovarian development was strongly influenced by total length, with larger females developing gravid ovaries earlier in the spawning season. Total length and fecundity were linearly related. The diet was dominated by various aquatic benthic invertebrate larvae and terrestrial insects. A comparison of the life histories of the two described species of *Gadopsis* shows them to be very similar.

APART FROM its description (Sanger 1984), a discussion on the use of artificial habitat to increase population size (Koehn 1987) and recent distributional information (Koehn 1990, Lintermans & Rutzu 1990), nothing has been published on the biology of the two-spined blackfish, *Gadopsis bispinosus*. Jackson (1978a, b) reported on several aspects of the biology of the related species *G. marmoratus* Richardson, including habitat preference, feeding, spawning and early life history. Collection of such information, which may be referred to as life history analysis, is of increasing importance given the recent level of interest in formal lists of the conservation status of Australian freshwater fish (Cadwallader et al. 1984, Harris 1987, Koehn & Morrison 1990) and in the management of wild populations of native fish for conservation purposes. In combination with detailed distributional data, life history analysis can provide a firm biological basis for decisions on both conservation status and management.

The life history of *G. bispinosus* is of interest not only because of the relatively recent discovery of the species, its somewhat restricted distribution and apparent abundance in streams inhabited by salmonids (Koehn 1990), but also because there is the opportunity for a comparison with the work of Jackson (1978a, b). Such a comparative approach may reveal factors of general relevance to management guidelines for *Gadopsis* species.

In order to examine the life history of *G. bispinosus*, a population was investigated in the upper reaches of King Parrot Creek (a tributary of the Goulburn River in the Murray River system), approximately 8 km downstream from Kinglake West, Victoria (37°52'S, 145°23'E). King Parrot Creek is typical of the streams in which this species is found: cool and clear with a cobble substrate.

MATERIALS AND METHODS

Physical data on mean monthly discharge and water temperature in King Parrot Creek were obtained from Rural Water Commission records from the Flowerdale water quality gauging station, situated about 10 km downstream of the study site. Samples of fish were collected with a portable DC electroshocker at approximately monthly intervals over a period of two years. They were killed in a solution of benzocaine and preserved in 4% formaldehyde.

Total length (TL) was measured to the nearest mm and total wet weight to the nearest 0.1 g. Fish were sexed by macroscopic gonadal examination. Males had a single, small, nodular, pinkish testis; females had a single, anteriorly bilobed, whitish to yellow ovary, within which developing oocytes could be seen. Juveniles had little or no gonadal tissue present; if present it was not obviously testicular or ovarian. Ovaries were dissected from preserved specimens, blot-

ted dry, and weighed to the nearest 0.001 g. The Gonadosomatic Index (GSI) was calculated by expressing ovary weight as a percentage of total body weight. Mean egg diameter (to the nearest 0.1 mm) was determined microscopically with the aid of a graduated scale. If mean egg diameter was at least 2.0 mm all eggs were dissected from the ovary and counted. Such ovaries were arbitrarily considered to be gravid. The stomach contents of several samples were examined under a stereo microscope. Individual food items were assigned to food categories broadly matching those used by Jackson (1978b), except that all aquatic Coleoptera were combined in a single category instead of two, and three new categories were used for food items not covered by Jackson's categories. These new categories are Decapoda for freshwater crayfish and *Paratya* sp., Isopoda for the semi-aquatic oniscoids, and galaxiids for the native fish *Galaxias olidus*. The composition of the diet was analysed by the occurrence, number and dominance methods as described by Hynes (1950). For comparison with the work of Jackson (1978b), the rank method of Pollard (1973) was also used. Although it is recognised that these methods of analysis are inherently biased in one way or another, use of several methods concurrently should reveal important components of the diet of *G. bispinosus*. Statistical analyses were performed with BMDP statistical software (Dixon 1983).

RESULTS

All samples were collected from a 100 m long section of the creek chosen because of its accessibility. The river bed in this section comprised stones varying in size from coarse gravel providing little in the way of cover, to cobbles providing adequate cover for fish. Additional instream cover was provided by several fallen logs and branches, and undercut banks in riffle regions and on the outer bank of bends. *Gadopsis bispinosus* was common in all habitats where adequate cover was present. The species was encountered infrequently in open water or over more homogeneous substrates without cover. The two exotic species *Salmo trutta* and *Perca fluviatilis* and the native species *Galaxias olidus* were also collected from this section of King Parrot Creek during the study. Of these species, only *S. trutta* was common.

Mean monthly discharge varied markedly over the two year sampling period (Fig. 1); however, variation followed a regular pattern of

high flows (more than 100 ML.day⁻¹) in late winter and early spring, and low flows (less than 20 ML.day⁻¹) in late summer and autumn. Water temperature ranged between 8.5°C in mid winter and 24.5°C in mid summer (Fig. 1).

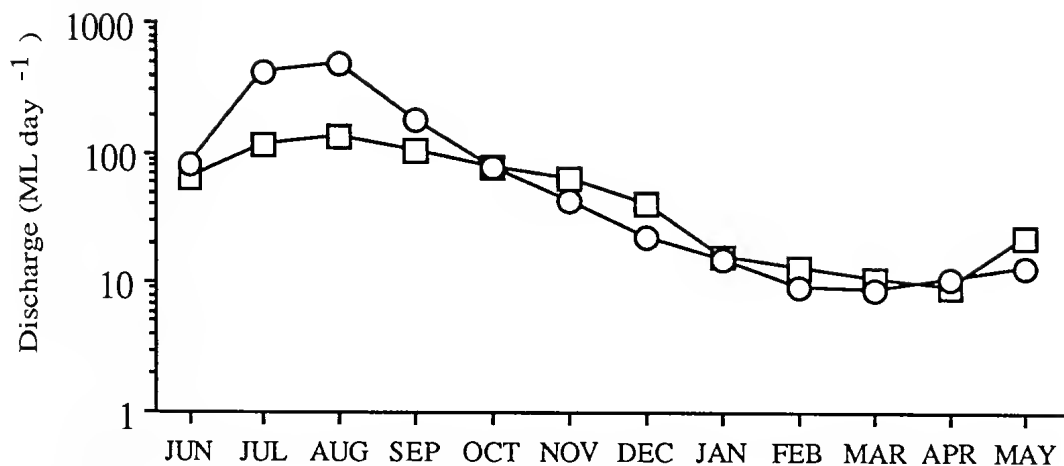
Length-frequency data for the entire sample ($n = 1054$) and for seasonal samples are given in Fig. 2. Mean TL for the entire sample (Fig. 2A) is 111 mm (range = 20 to 257 mm). The 40 mm (30–49 mm) to 180 mm (170–189 mm) size classes comprise more than 90% of the total sample; the 220, 240 and 260 mm size classes comprise less than 2%. Seasonal variation in maximal and mean TL is small (Fig 2B). The appearance of the smallest size class (20 mm; 10–29 mm) in the summers of 1981 and 1982 indicates that recruitment of juveniles occurred in this period. In the autumn of both these years a strong 0+ cohort can be seen as the first peak on the histograms.

The relationship between total length and total weight for the entire sample, and for males and females separately, is indicated in Table 1. Females were slightly heavier than males (ANCOVA; $p < 0.01$).

Most individuals less than 100 mm TL were classified as juveniles ($n = 385$), with 57 females and 19 males comprising the remainder. The difference between the number of males and females in these small fish is due to the fact that females are easier to recognise than males; female gonads are larger than those of males, so that females were easier to distinguish from juveniles than were males. The sex ratio of fish greater than 100 mm TL ($n = 288$ males, 306 females) did not differ significantly from 1:1 (Chi square = 0.545, $p < 0.75$).

Females with gravid ovaries were found between September and December in 1980, and between October and December in 1981 (Table 2). The values of ΔN in Table 2 show how many females in each monthly sample were larger than the largest gravid female in that sample. These values increased during the spawning period in both years. Thus, early in the spawning season the largest gravid females tended to be the largest females in the sample. As the spawning season progressed, the larger females possessed very small developing ovaries ($GSI < 1.1$) and smaller gravid females were present ($GSI > 9.4$). In the January samples, all adult females had ovaries in the early stages of development (GSI values normally < 1). Water temperature rose rapidly from about 12°C to 17°C between October and November in 1980, and between November and December in 1981. Thus, it

A



B

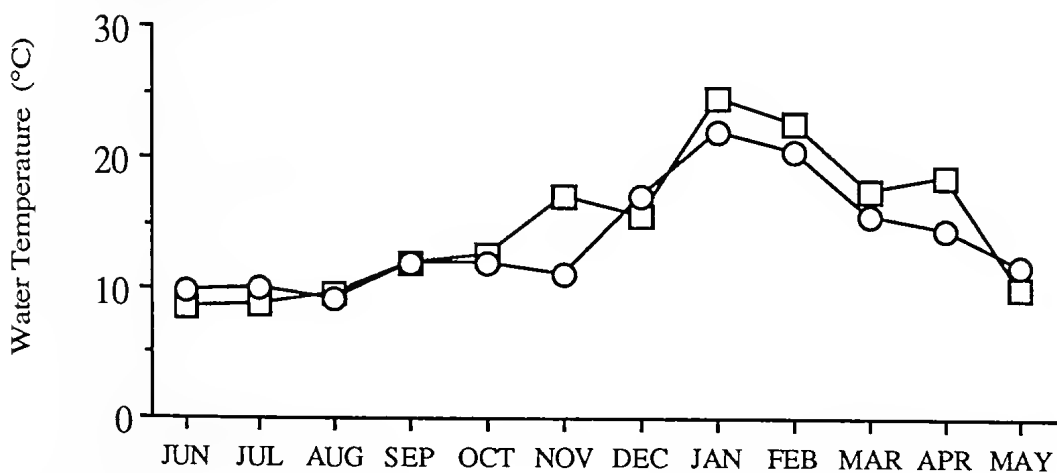


Fig. 1. Environmental characteristics of King Parrot Creek between June 1980 and May 1982. A, mean monthly discharge in ML.day⁻¹. B, water temperature in °C. Open squares 1980-81; open circles 1981-82.

	Regression equation	n	r	p
Total sample	$\text{Log}_{10} W = 2.856 \text{ Log}_{10} TL - 4.805$	1054	0.994	<0.001
Females	$\text{Log}_{10} W = 2.757 \text{ Log}_{10} TL - 4.589$	363	0.990	<0.001
Males	$\text{Log}_{10} W = 2.751 \text{ Log}_{10} TL - 4.587$	307	0.986	<0.001

Table 1. Relationship (linear regression) between total length (TL) and weight (W) of *Gadopsis bispinosus* in King Parrot Creek; n = sample size, r = correlation coefficient, p = probability value for r.

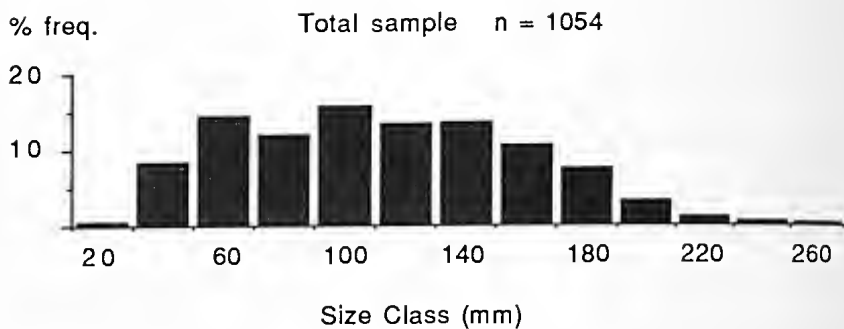
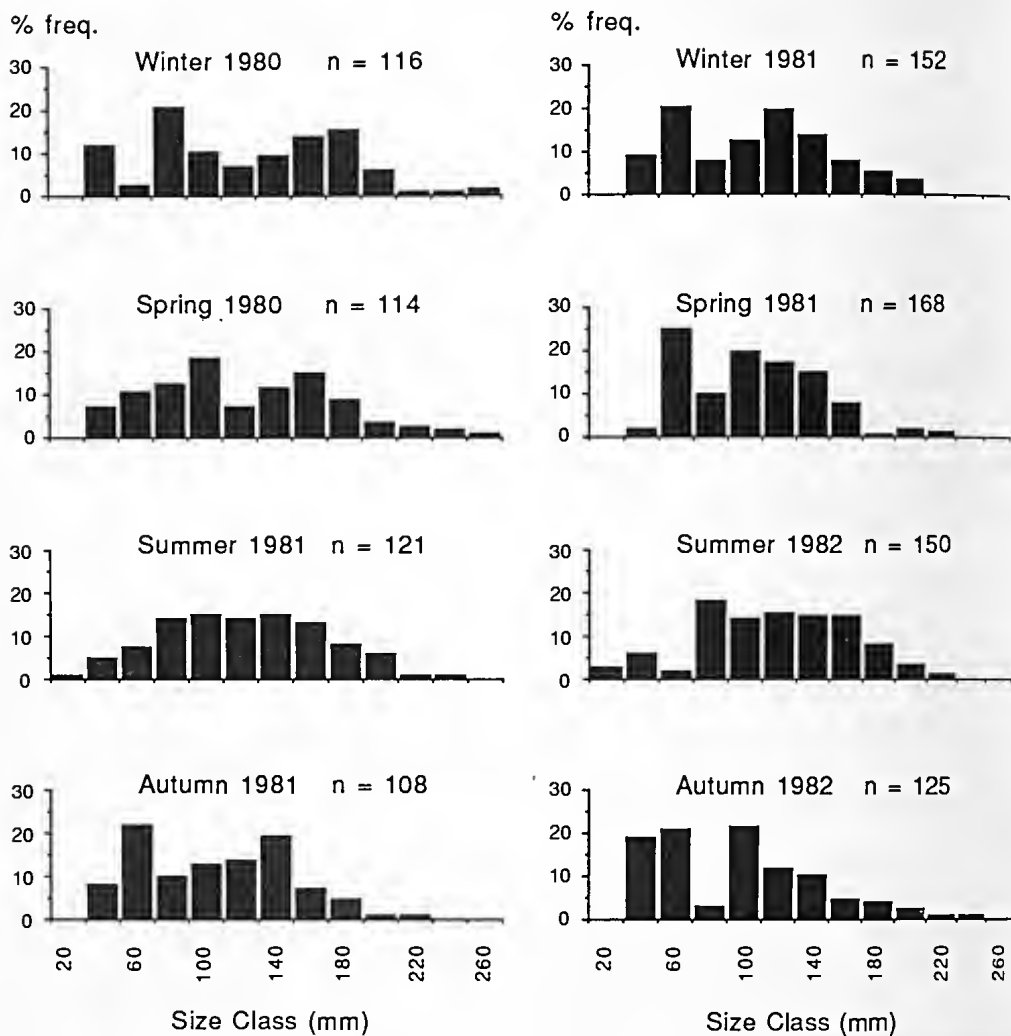
A**B**

Fig. 2. Length-frequency histograms for (A) the total sample and (B) seasonal samples of *Gadopsis bispinosus* in King Parrot Creek.

Month	Water temp. (°C)	Total sample		Largest female		Largest gravid female		ΔN
		N	Mean GSI	TL	GSI (mm)	TL	GSI (mm)	
September 80	11.9	15	2.22	198	5.77	198	5.77	0
October 80	12.6	11	5.12	207	11.84	207	11.84	0
November 80	17.0	9	4.90	230	0.95	158	10.48	4
December 80	15.5	17	1.36	242	0.04	116	15.40	10
January 81	24.5	22	0.33	242	0.38	no gravid females		-
September 81	11.9	17	1.05	196	2.45	no gravid females		-
October 81	11.9	13	1.12	177	9.64	177	9.64	0
November 81	11.0	23	3.20	194	0.01	152	9.46	2
December 81	17.0	18	6.62	178	1.02	117	16.3	7
January 82	22.0	13	0.38	184	0.42	no gravid females		-

Table 2. Seasonal variation in GSI values and length of gravid females; N = number of females in monthly sample, ΔN = number of females larger than largest gravid female.

Category	Occurrence	Number	Dominance	Rank
Trichoptera	76.0	15.9	24.4	21.6
Diptera	67.6	31.1	8.3	15.3
Ephemeroptera	81.1	33.3	29.4	24.5
Plecoptera	33.5	6.9	3.2	8.7
Coleoptera	27.3	2.8	3.0	6.9
Hemiptera	4.7	0.4	0.9	0.9
Odonata	4.0	0.3	1.5	1.2
Megaloptera	1.1	<0.1	1.2	0.3
Amphipoda	14.6	3.1	3.0	3.8
Decapoda	6.5	0.4	3.4	1.8
Isopoda	1.5	0.1	0.4	0.3
Oligochaeta	4.7	0.3	3.1	1.5
Arachnida	1.1	<0.1	0.0	0.3
Terrestrial	28.4	4.4	15.7	8.7
Fish eggs	1.1	0.5	0.8	0.5
<i>Galaxias olidus</i>	0.4	<0.1	0.4	0.2
Miscellaneous	11.6	0.3	1.9	3.2

Table 3. Stomach contents of *Gadopsis bispinosus* from King Parrot Creek; n = 275. Occurrence = percentage of stomachs in which each category occurs; number = percentage contribution of each category to total number of food items; dominance = percentage of stomachs in which each category dominated volumetrically; rank = percentage composition of diet by rank method.

appears that the spawning season extends over several months from about October to December, that large females spawn earlier than small females, and that the onset of spawning coincides with an increase in water temperature in spring.

The number of eggs in gravid ovaries ranged between 84 (fish TL = 121 mm) and 350 (fish TL = 207 mm). The relationship between total length and fecundity is described equally well by the relationships:

$$\begin{aligned} \text{Fecundity} &= 2.50 \text{ TL} - 205; r^2 = 0.74; p < 0.001; \\ &\text{and} \\ \text{Log}_{10} \text{ Fecundity} &= 2.16 \text{ Log}_{10} \text{ TL} - 2.50; r^2 = 0.72; \\ &p < 0.001 \end{aligned}$$

The exponential relationship is probably more appropriate because the number of eggs in an ovary is governed more by the volume of the ovary (a cubic measure) than by its length. Nevertheless, the significance of the two correlations is identical.

Table 3 summarises the results of the analysis of the stomach contents of 275 fish taken from 14 samples spaced at approximately two-monthly intervals over the sample period. The dietary importance of several groups of benthic insect larvae is evident from the table, with ephemeropteran, trichopteran and dipteran nymphs and pupae predominating in the diet assessed by all four methods of analysis. Terrestrial arthropods and the aquatic groups Plecoptera, Coleoptera, and Amphipoda were also important in the diet. The method-dependent differences between the scores for each category reflect the biases inherent in the methods. For example, whereas dipteran larvae occurred frequently and were often numerous, they were usually small and did not dominate many guts volumetrically. Thus, dipteran larvae scored higher values in the occurrence and number methods than in the dominance and rank methods.

Fish eggs, almost certainly eggs of *G. bispinosus*, were found in the diet of a few fish in December 1981 and 1982, supporting the suggestion that spawning had taken place at this time.

The major aquatic groups, i.e. Ephemeroptera, Trichoptera, Diptera, Plecoptera and Coleoptera, were relatively important in all

monthly samples (Table 4). Terrestrial food was more important in the spring and summer months, perhaps reflecting a greater availability during this period.

DISCUSSION

Gadopsis bispinosus is the most abundant species of fish in the upper reaches of King Parrot Creek. Koehn (1987) found that it was also the most abundant species of fish in the upper reaches of the Ovens River, Victoria, and has shown experimentally that an increase in the amount of instream cover led to an increase in abundance of the species in that stream. It appears likely, therefore, that *G. bispinosus* would be abundant in most north-eastern Victorian streams with abundant instream cover (especially accumulations of cobbles and fallen timber) and relatively cool, clear water.

The length-frequency distributions confirm that, at least in King Parrot Creek, *G. bispinosus* is a small to medium-sized species (observed maximum TL 257 mm). The causes of adult mortality are unknown, apart from predation by *Salmo trutta* (Sanger 1984). It has been suggested that there is a correlation between the presence of *S. trutta* and a decline in the abundance and diversity of the native fish fauna in

Sample date	n	Ephemeroptera	Trichoptera	Diptera	Plecoptera	Coleoptera	Hemiptera	Odonata	Amphipoda	Decapoda	Isopoda	Annelida	Terrestrial	Fish eggs	<i>G. olidus</i>	Miscellaneous
24.5.80	12	22.9	11.1	21.5	11.7	3.9	-	5.6	13.6	2.3	-	-	3.2	-	-	4.2
21.8.80	18	16.0	10.3	19.0	9.5	9.9	2.7	1.3	12.3	4.2	0.5	-	5.7	-	-	7.1
24.9.80	12	24.2	9.0	27.0	2.6	6.6	-	-	8.8	-	-	2.8	15.6	-	-	3.3
20.10.80	13	22.7	12.5	21.0	20.0	5.2	-	-	-	-	-	4.5	12.7	-	-	1.4
22.12.80	20	22.8	15.1	25.0	4.8	7.8	-	-	-	1.8	-	-	7.5	5.1	-	10.2
20.2.81	18	20.0	17.4	27.9	-	9.6	-	2.1	-	-	-	-	19.8	-	-	3.2
22.4.81	23	24.0	27.6	19.4	3.5	12.1	-	-	-	1.4	-	-	4.9	-	-	7.1
19.5.81	23	18.9	22.9	25.6	11.9	2.1	-	1.9	4.9	1.6	-	-	2.6	-	-	7.7
21.6.81	21	18.4	13.6	29.4	14.0	5.4	1.8	0.6	1.8	3.2	-	1.8	7.2	-	-	2.8
16.9.81	20	23.8	11.8	28.6	16.3	4.5	1.4	-	-	-	1.4	2.1	4.1	-	2.1	4.1
24.12.81	17	24.9	16.6	25.3	8.1	9.0	0.6	-	-	2.3	-	3.7	6.1	2.3	-	1.5
22.2.82	34	15.1	10.3	16.7	7.3	8.5	2.4	3.8	8.9	4.6	-	3.4	15.4	-	-	3.8
23.3.82	26	20.1	18.2	32.2	1.4	6.0	2.9	0.6	-	1.8	1.2	1.6	12.5	-	-	2.1
17.5.82	18	27.9	17.3	25.3	10.2	5.3	1.8	1.2	2.3	2.3	1.6	-	4.0	-	-	0.8
Total % rank	275	21.6	15.3	24.5	8.7	6.9	0.9	1.2	3.8	1.8	0.3	1.5	8.7	0.5	0.2	3.2

Table 4. Seasonal comparison of the diet of *Gadopsis bispinosus* from King Parrot Creek, analysed by the rank method.

Australian streams (Tilzey 1976, Jackson & Williams 1980). The presence of *S. trutta* does not appear to affect the abundance of *G. bispinosus* in the present study. Indeed, the recent study by Koehn (1987) suggests that the amount of instream cover is a more serious limiting factor. Similarly, *G. marmoratus* has been found to cope adequately with the competitive pressure of coexistence with *S. trutta* in some Victorian streams (Jackson 1978b, Jackson & Williams 1980), and the abundance of *G. marmoratus* in some Victorian and Tasmanian streams has been shown to be correlated more closely with instream cover and low flows than with any other habitat attributes (Cadwallader 1979, Koehn 1986, Davies 1989).

The timing of recruitment of *G. bispinosus* appears to be similar to that of *G. marmoratus* found by Jackson (1978a) and Koehn (unpublished data) in some Victorian streams. In both those studies spawning activity was found between mid-November and mid-December. Jackson (1978) concluded from aquarium observations that the time from spawning to active feeding was about eight weeks, and suggested that recruitment should have occurred in January and February in the McKenzie River in 1976. Recruits were first detected in the King Parrot Creek population of *G. bispinosus* in February 1981 (mean TL 39.9 mm) and January 1982 (mean TL 27.1 mm). The water temperatures in King Parrot Creek from November to February are within the range reported by Jackson (1978a) for the McKenzie River, and by Koehn (unpublished data) for Armstrong Creek. Although in the present study the spawning period of *G. bispinosus* has been determined indirectly from ovarian condition and from predation on eggs, it is similar to that reported for *G. marmoratus* and shows a similar association with increasing water temperatures. The maximum diameter of ovarian eggs in *G. bispinosus* (3.5–4.0 mm) and of fertilized eggs in *G. marmoratus*, and the correlation of fecundity with total length are also similar (Jackson 1978a, Koehn unpublished data). The relationship between total length and month of maturity has not been reported previously for species of *Gadopsis*.

At the taxonomic level employed in the present study, the diet of *G. bispinosus* is very similar to that of *G. marmoratus* in the Aberfeldy River, as described by Jackson (1978b). Terrestrial insects were more important than dipteran larvae in the diet of *G. marmoratus* in the Aberfeldy River, but the influence of different sample

dates, the size range of fish used and the availability of the different prey types could all have influenced this result. The presence of freshwater crayfish, a galaxiid fish and fish eggs also distinguish the diet of *G. bispinosus* from that of *G. marmoratus* in the Aberfeldy River, although these items do not comprise a major part of the diet of *G. bispinosus*. The seasonal composition of the diet of *G. bispinosus* was relatively stable, no distinct seasonal peaks in rank values for any food category being evident in the data. The seasonal composition of the diet of *G. marmoratus* in the Aberfeldy River was also relatively stable.

The concurrence of life history characteristics of *G. bispinosus* and *G. marmoratus* should enable the formulation of overall guidelines for the management of wild populations of *Gadopsis* species. The importance of instream cover to both species has already been demonstrated (Jackson 1978a, b; Koehn 1986, 1987; Davies 1989). Other features which appear to be important are a spring increase in water temperature which correlates with the onset of spawning, and the heavy reliance on benthic invertebrates in the diet of both species. Environmental degradation, including an artificial lowering of spring and early summer water temperatures through release of cold impoundment water, a decrease in the amount of instream cover either from de-snagging or siltation, and disruption of the benthic invertebrate fauna through substrate disturbance or the introduction of toxins into streams, could thus be expected to have a detrimental effect on stream populations of *Gadopsis* species.

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DISTRIBUTION AND CONSERVATION STATUS OF THE TWO-SPINED BLACKFISH *GADOPSIS BISPINOSUS* IN VICTORIA

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In Victoria, the two-spined blackfish, *Gadopsis bispinosus*, is restricted to the upper reaches of streams north of the Great Dividing Range in the eastern part of the state, at altitudes of 200-760 m. The western limit of the species' range appears to be King Parrot Creek, about 50 km north-east of Melbourne; the northern and eastern parts of its range extend into New South Wales. Recent surveys and the re-examination of *Gadopsis* specimens collected before *G. bispinosus* was described in 1984 show that *G. bispinosus* is common and abundant throughout its range, with more than 2087 specimens having been recorded from 55 sites. Consequently, the conservation status of this species in Victoria is revised to the category of 'restricted', i.e. "a taxon which is not presently in danger but which occurs in a restricted area".

THE GADOPSIDAE is a family of freshwater fish endemic to south-eastern Australia and containing two species in the genus *Gadopsis*. The freshwater blackfish, *Gadopsis marmoratus* Richardson, 1848, is widespread throughout Victoria and has been the subject of much research (Jackson 1975, 1978a, 1978b, 1981, unpublished data, Jackson & Llewellyn 1980, Jackson & Williams 1980, Koehn 1986, unpublished data). The two-spined blackfish, *Gadopsis bispinosus* Sanger, was described in 1984 after a detailed study of the taxonomy of the *Gadopsis* complex (Sanger 1984, 1986). *G. bispinosus* is distinguished from *G. marmoratus* by having two (range 1-3) instead of 11 (range 6-13) dorsal fin spines and by having a prominent white fringe on the dorsal, anal and caudal fins (Sanger 1984).

The present paper records the localities in Victoria where *G. bispinosus* has been collected. An assessment of conservation status is made on the basis of the abundance of the species at many sites, its distribution, its biological requirements and possible threats.

METHODS

Information on the distribution of *G. bispinosus* was obtained from specimen collections of the Fisheries Division and the Museum of Victoria, from recent surveys conducted by Fisheries Division staff, from recent publications (Sanger 1986, Brumley et al. 1987, Morison & Anderson 1987, Anderson & Morison 1989), and from two reliable but unconfirmed reports by an angler.

The surveys were conducted at 46 sites, many of them lying outside the range of *G. bispinosus* described in this paper, but these helped to establish the species' western limit of distribution.

Of the *Gadopsis* specimens held by the Fisheries Division and the Museum of Victoria, all those which had been collected before *G. bispinosus* was described and which had been previously identified as *G. marmoratus* were re-examined.

Abundance data available from many surveys were collated and, together with distributional data, were presented for discussion at a meeting convened at the Arthur Rylah Institute for Environmental Research on 12 August 1989 for the purpose of reviewing the conservation status of Victorian native freshwater fish (Koehn & Morison 1990).

RESULTS

G. bispinosus has been recorded from 55 sites in Victoria (Fig. 1, Table 1). The specimen from site 10 was collected in 1974 prior to the filling of Lake Dartmouth, so that this population can no longer be confirmed. One specimen in the Museum of Victoria (registration no. NMV A7982, recorded as being from the "Jamicon River, Victoria", presumably the Jamieson River) was collected on 11 December 1885. The species was also recorded by Sanger (1986) from unspecified localities in the Indi River, Snowy Creek (a tributary of the Mitta Mitta River) and the Catherine River (Ovens River Basin).

Site No.	Stream	Altitude (m)	Map. No.	Grid Ref.	Date	No. Specimens	Collector
1	Nariel Ck	500	8425	743 664	7.3.78	12	AB
2	Corryong Ck	300	8425	777 963	8.3.78	12	AB
3	Cudgewa Ck	400	8425	598 909	9.3.78	12	AB
4	Cudgewa Ck	280	8425	749 028	8.3.78	12	AB
5	Koetong Ck	360	8325	355 075	25-27.1.89	22	K
6	Bucheen Ck	480	8425	491 706	7.6.79	24	AB
7	Tallangatta Ck	300	8325	375 793	7.6.79	13	AB
8	Bundarra R.	760	8324	401 050	4.3.80	21	BT
9	Big R.	720	8324	412 167	1987	1	GP
10	Mitta Mitta R.	380	8424	512 522	2.2.74	1	NMV
11	Mountain Ck	460	8324	195 377	5.6.79	1	AB
12	Kiewa R.	320	8324	140 365	6.6.79	1	AB
13	Morses Ck	320	8224	981 336	23.5.79	25	AB
14	Buckland R.	380	8224	872 215	24.5.79	5	AB
15	Buckland R.	340	8224	863 278	1.6.87	4	*
16	Buckland R.	280	8224	905 385	4.4.78	6	AB
					24.5.79	12	AB
					18.3.80	33	AB
17	Ovens R.	260	8224	908 393	1984-87	86	JK
18	Ovens R.	220	8224	825 475	5.4.78	6	AB
19	Ovens R.	220	8224	785 498	17.3.80	37	AB
20	Buffalo R.	360	8224	734 144	6.4.78	31	AB
					7.6.87	1	K
21	Buffalo R.	280	8224	696 230	13.2.89	77	K
22	Buffalo R.	280	8224	695 256	8.6.87	1	K
					16.2.89	25	K
23	Rose R.	460	8224	586 093	7.5.79	32	AB
24	Dandongadale R.	320	8224	647 232	9.5.79	24	AB
					2.4.80	39	AB
25	Dandongadale R.	300	8224	669 263	22.2.89	7	K
26	Dandongadale/Rose R.	300	8224	671 266	10.5.79	24	AB
					1.4.80	27	AB
					22.2.89	8	K
27	Buffalo R.	280	8224	701 276	6.4.78	2	AB
					17.2.89	4	K
28	Buffalo R.	260	8224	705 370	20.2.89	1	K
29	Buffalo R.	240	8224	700 392	20.2.89	9	K
30	Stony Ck	300	8124	490 232	31.10.83	3	AS
31	King R.	480	8124	489 118	16.2.89	100	AB
32	King R.	380	8124	460 148	1.4.80	22	AB
33	King R. (West)	360	8124	428 192	15.12.79	26	AS
34	King R.	200	8124	482 466	7.4.78	22	AB
					30.3.80	10	AB
35	15 Mile Ck	580	8124	355 204	13.3.79	15	AB
36	15 Mile Ck	480	8124	355 253	18.3.89	2	*
37	Ryans Ck	340	8124	303 357	14.3.79	1	AB
38	Hollands Ck	360	8124	228 239	28.11.79	34	AB
					8.6.89	2	K
39	Delatite R.	420	8123	323 922	11.5.89	26	K
40	Delatite R.	380	8123	242 888	10.5.89	26	K
41	Delatite R.	380	8123	226 882	9.5.89	6	K
42	Delatite R.	320	8123	203868	3.5.89	1	K
43	Delatite R.	320	8123	165 857	5.5.89	1	K
44	Howqua R.	360	8123	299 794	18.4.78	1	AB
45	Jamieson R.	360	8123	265 725	18.4.78	3	AB
46	Goulburn R.	380	8123	302 621	19.4.78	4	AB
47	Royston R.	400	8023	990 684	2.5.89	4	*
48	Rubicon R.	360	8023	981 700	3.5.89	1	*
49	Acheron R.	400	8022	844 403	11.12.87	2	*

Site No.	Stream	Altitude (m)	Map. No.	Grid Ref.	Date	No. Specimens	Collector
50	Murrindindi R.	360	8023	725 600	27.6.89	1	*
51	Yea R.	360	7922	605 468	27.6.89	1	*
52	Kalatha Ck	240	7923	633 590	27.6.89	1	*
53	King Parrot Ck	360	7923	450 560	3.11.79	20	AS
					20.10.80	7	AS
					1.6.87	5	*
					5.5.89	22	*
54	King Parrot Ck	360	7923	455 563	26.10.78	2	PJ
55	King Parrot Ck	280	7923	483 658	11.10.78	5	PJ

Table 1. Sites sampled and details of collections made. AB = Baxter 1985, AS = Sanger 1984, BT = B. Tunbridge, GP = G. Paras (angling record), JK = Koehn 1987, K = Kaiela Fisheries Research Station, NMV = Museum of Victoria, PJ = P. Jackson, * = this study.

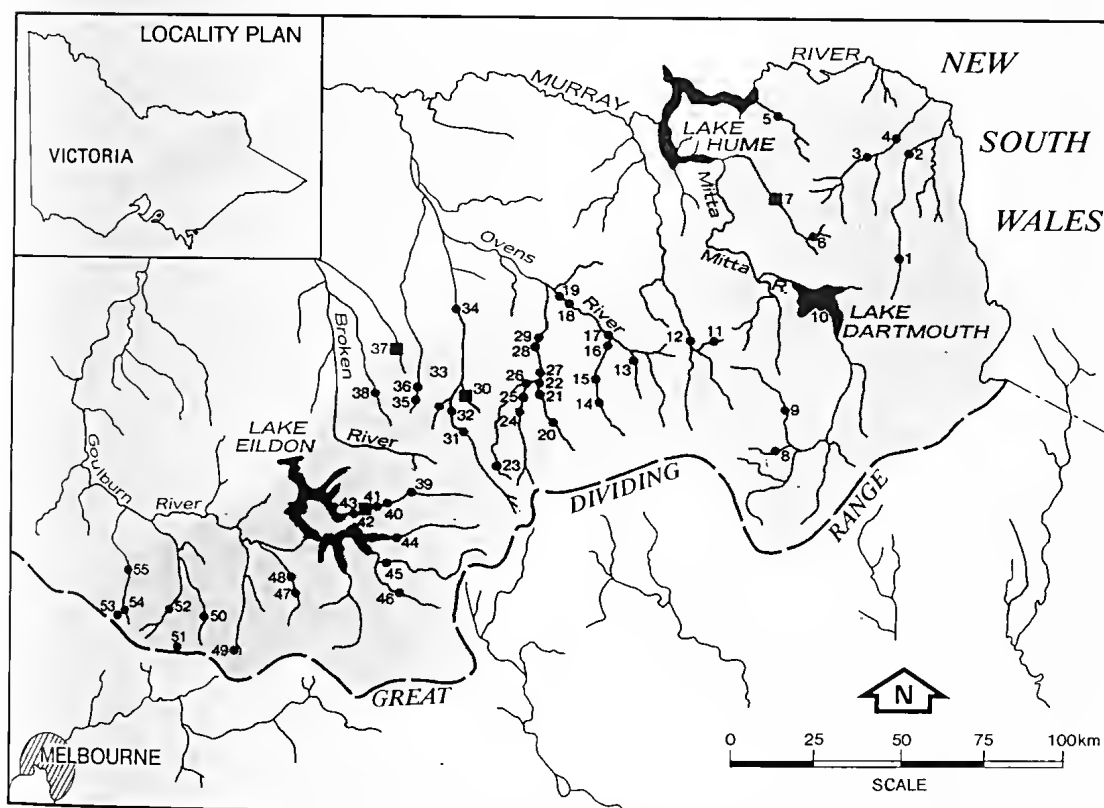


Fig. 1. Site localities and distribution of *Gadopsis bispinosus* in Victoria; squares indicate sites where *G. mar-moratus* occurs with *G. bispinosus*.

G. bispinosus has also been collected recently from the Cotter River in the Australian Capital Territory (Lintermans & Rutzu 1990), and the Australian Museum contains specimens from the Gehee River (Kosciusko National Park,

January 1975) and Micalong Creek (upstream of Wee Jasper, 1931) in New South Wales (T. Gill, Australian Museum, Sydney, pers. comm.).

All sites in Victoria are in the upper reaches of streams, but *G. bispinosus* was absent from sev-

eral headwater tributaries where cascades and very high water velocities were present. The specimens ranged in size from young-of-the-year fish with a total length of 45 mm (site 48) to 275 mm (site 47). Although sites were not sampled quantitatively, *G. bispinosus* was considered to be abundant at many of them. More than 50 specimens were collected at three sites and 20 or more specimens at 24 sites; in addition, Sanger (1990) collected a total of 1055 specimens from site 53 on King Parrot Creek between June 1980 and June 1982.

At sites for which records of other species were available, *G. bispinosus* was associated with brown trout, *Salmo trutta*, at 95% of sites; with rainbow trout, *Oncorhynchus mykiss*, at about 50% of sites; and with redfin, *Perca fluviatilis*, at about 50% of sites. Other species collected with *G. bispinosus* include Murray cod, *Maccullochella peelii*; trout cod, *M. macquariensis*; *Galaxias* spp., particularly, *G. olidus*; Australian smelt, *Retropinna semoni*; southern pigmy perch, *Nannoperca australis*; and goldfish, *Carassius auratus*. *Gadopsis marmoratus* occurred in sympatry with *G. bispinosus* at sites 7, 30, 37, and 42 but was found without *G. bispinosus* in a small sample upstream of site 37. *G. marmoratus* was common at downstream localities along the northern and western edges of the range of *G. bispinosus*.

DISCUSSION

In Victoria, *G. bispinosus* is restricted to the upper reaches of streams in the north-eastern part of the state, in a band covering a maximum distance of about 100 km from the ridge of the Great Dividing Range (Fig. 1). The western limit of the range appears to be King Parrot Creek, about 50 km north-east of Melbourne. The northern and eastern parts of the species' range extend into New South Wales. The distribution in Victoria encompasses that previously suggested by Sanger (1986).

G. bispinosus is common and abundant throughout most of its range in Victoria and appears under no immediate threat. Consequently, despite the lack of historical population data, it is suggested that the conservation status of *G. bispinosus* in Victoria should be revised to the category of "restricted", in that it is a taxon which is "not presently in danger but which occurs in a restricted area" (Koehn & Morison 1990). This suggestion is consistent with the view of Sanger (1984) that *G. bispinosus* is not a rare or endangered species and should

not be afforded greater protection than *G. marmoratus*. The latter is a popular angling species in southern Victoria (Barnham 1983, Koehn 1984), but *G. bispinosus* is much smaller and is unlikely to be a major target species of anglers, although it may be caught incidentally.

Cadwallader et al. (1984) included *G. marmoratus* in Category E ("requiring careful monitoring in Victoria"), partly because the taxonomy of *Gadopsis* was under review. For the same reason, the recent conservation status review (Koehn & Morison 1990) included *G. marmoratus* in the equivalent category of "indeterminate".

Two distinct forms of *G. marmoratus* (southern and northern) have been referred to by recent workers (Ovendon et al. 1988, Sanger 1986) and these may be recognised as separate species in the future (Sanger pers. comm.). *G. marmoratus* (northern form) has been found with *G. bispinosus* at four of the sites sampled, and Sanger (1984) previously reported sympatry between these species in the upper King River. Although both species appear to have similar life history strategies, no evidence for interspecific hybrids has been found (Sanger 1984). Sanger (1986, 1990) found *G. bispinosus* to have an extended spawning period of November–February, similar to that of *G. marmoratus* (Jackson 1978a, Koehn unpubl. data). It is assumed that spawning sites of *G. bispinosus* are similar to those of *G. marmoratus*; that is, inside hollow logs (Jackson 1978a, Koehn unpubl. data) and possibly among rocks (Proebsting et al. 1974). Large numbers of *G. bispinosus* (including young-of-the-year-fish) have been collected amongst cobbles and boulders in stream reaches without wood debris and logs, and it is likely such areas may be used as spawning sites.

The distribution of *G. marmoratus* and *G. bispinosus* in northern streams appears to be related to the habit and habitat requirements of the two species. *G. marmoratus* is usually associated with instream cover, showing a preference for habitats where water velocities are low and logs and wood debris abundant (Jackson 1978a, 1978b, Koehn 1986). Such habitats tend to be in the lower, slower-flowing reaches of northern streams. *G. bispinosus* has mostly been found in clear streams with rocky bottoms where water velocities may be relatively high. The species was usually found to be utilizing some form of instream cover, often cobbles and boulders as wood debris was not always present. The species was not common in open water or in more

homogeneous substrates (Sanger 1990). Koehn (1987) found that boulders placed in the Ovens River markedly increased the numbers of *G. bispinosus* present because the boulders created a range of habitats that could be used as shelter from the fast water velocities. Being a smaller, more slightly built species than *G. marmoratus* (southern form), *G. bispinosus* appears to be able to utilize such instream niches more effectively. *G. bispinosus* was not found in the headwaters of many streams that, although providing sheltered areas, also contained areas of fast-flowing or cascading water.

Several other freshwater fish genera include two closely related species, one of them inhabiting the upper reaches of a river system and the other inhabiting the lower reaches. The Murray cod, *Maccullochella peelii*, inhabits the warmer, slower, lowland reaches of streams in the Murray Darling River system, whereas the trout cod, *M. macquariensis*, is better adapted to cooler upland reaches (McDonald 1978, Cadwallader 1979, Cadwallader & Gooley 1984). The distributions of the golden perch, *Macquaria ambigua*, and the closely related Macquarie perch, *M. australasica*, show a similar relationship (McDonald 1978, Cadwallader 1979, 1981), as do the distributions of the flat-headed galaxias, *Galaxias rostratus*, and the Mountain galaxias, *G. olidus*, in the Murray-Darling River system (Cadwallader 1979, Cadwallader & Backhouse 1983).

Galaxias olidus was present at many of the Victorian localities surveyed and would be expected to occur throughout much of the range of *G. bispinosus*. The distribution and abundance of *G. olidus* has been severely reduced, however, by interactions with brown trout, *S. trutta*, and mutually exclusive populations of the two species have been documented (Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Davies 1983, Jackson & Williams 1980, Koehn unpubl. data). Regular stocking of *S. trutta* by the Fisheries Division occurs throughout the range of *G. bispinosus* (Barnham 1989), and because the upper reaches of streams are particularly suited to both species, interaction between them may be expected to be more intense than between *G. marmoratus* and *S. trutta*. Sanger (1984) noted predation by *S. trutta* as a cause of mortality in *G. bispinosus* but reported that *G. bispinosus* remained abundant. Jackson (1978a, 1981) and Jackson & Williams (1980) considered that, although there was dietary overlap between *G. marmoratus* and

S. trutta, they avoided direct competition by occupying different habitats.

The sympatric relationship between *G. bispinosus* and *G. marmoratus* and the interaction of the former with *S. trutta* are worthy of further study. Further information is also needed on the habitat and spawning requirements of *G. bispinosus*, as environmental degradation such as sedimentation and habitat alteration are likely to pose the greatest threat to the species.

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BYTHOCYPRIDIDAE (OSTRACODA) FROM THE MIOCENE OF THE PORT PHILLIP AND WESTERN PORT BASINS, VICTORIA

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Six bythocyprid species have been identified from the Lower to Middle Miocene of the Port Phillip and Western Port Basins. They are *Bythocypris* (*Bythocypris*) *subrectangulata* sp. nov., *Bythocypris* (*Bythocypris*) cf. *affinis* (Brady), *B. (B.)* sp. A, *B. (B.)* sp. B, *Anchistrocheles praebensoni* sp. nov. and *Orlovibairdia mooraboolensis* sp. nov. In a review of the Bythocyprididae, the new subgenus *Bythocypris* (*Bythotriangularia*) and the new genus *Bythopussella* are named for species occurring outside the Port Phillip and Western Port Basins.

THE BYTHOCYPRIDIDAE is a family of ostracods that is well represented in late Tertiary rocks of the Port Phillip and Western Port Basins, Victoria. In this paper, material of bythocypridids recently recovered from the Batesford Limestone and from the Fyansford and Sherwood Formations is described. A general review of the family is integrated within the systematic taxonomy and includes the description of a new subgenus and a new genus for forms occurring outside the region. The lithostratigraphy of the study area and sample localities are outlined by Warne (1987, 1988, 1989).

Within the Port Phillip and Western Port Basins, bythocypridids reached their maximum abundance during the late Early to early Middle Miocene. This abundance is considered to be due to the relatively warm aquatic temperatures and the wide range of palaeoenvironments that existed at that time (Warne, 1987, 1988, 1990). These conditions coincided with generally high global sea levels (Haq et al. 1987). The maximum extent of the marine incursion in the Port Phillip and Western Port Basins, as indicated by Mallett & Holdgate (1985), Carter (1985) and Warne (1987), presumably led to greater ranges in palaeodepths than at other times in the late Tertiary, generating a comparatively large number of depth-related palaeoecological niches.

SYSTEMATIC PALAEONTOLOGY

Type and figured specimens are housed in the invertebrate palaeontological collection of the Museum of Victoria (NMV P122202–P122212). Other specimens are housed on

assemblage slides under the registered numbers NMV P122682–P122763. Locality details for assemblage slides are recorded in Warne (1989) and at the Museum of Victoria. Outcrop samples were approximately 0.5 kg. dry weight. The abbreviations RV = right valve, LV = left valve, L = length, H = height are used throughout the text.

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA G. W. Müller, 1894
Suborder PODOCOPA Sars, 1866
Superfamily BAIRDIACEA Sars, 1866
Family BYTHOCYPRIDIDAE Maddocks, 1969

Remarks. Cainozoic Bythocyprididae are here distinguished from the Bairdiidae by their adductor muscle scar pattern, which usually includes four scars when undivided, and by the generally compressed nature of their carapace in dorsal view. I assign eight Cainozoic genera and subgenera to the Bythocyprididae, namely *Bythocypris* (*Bythocypris*) Brady, 1880, *Bythocypris* (*Bythotriangularia*) subgen. nov., *Anchistrocheles* Brady & Norman, 1889, *Bythopussella* gen. nov., *Danipussella* Wouters, 1988, *Orlovibairdia* McKenzie, 1978, *Pussella* Danielopol in Maddocks, 1976 and *Zabythocypris* Maddocks, 1969. Danielopol (1976), Maddocks (1976) and Wouters (1988) arranged some of these genera into the subfamilies Bythocypridinae Maddocks, 1969 and Pussellinae Danielopol, 1976, mainly on the basis of differences in the shape of the brushlike organ and the number of limb bristles.

As in the Bairdiidae (Warne 1988), gradational and mosaic relationships abound within the Bythocyprididae. In this paper I attempt to refine the definitions of many bythocyprid genera. This is possible because members of the Bythocyprididae display a slightly greater degree of non-gradational species-group clustering than do the Bairdiidae. These bythocyprid species groups also have a more uniform environmental distribution than do presently recognised bairdiid genera.

The Bairdiidae and the Bythocyprididae are not distinguished by consistent or simple morphological differences. A number of forms, in particular those belonging to *Bythopussella* gen. nov., have carapace and soft part characters that are either intermediate in structure between the two families, or are unusually combined in the one form. For example, species such as *Bythopussella aculeata* (Müller, 1908), *B. aff. aculeata* of Maddocks (1969) and *B. sp. A* (Cronin, 1983) have muscle scar patterns and compressed carapaces typical of adult bythocypridids, but have lateral carapace outlines and anatomical features akin to juvenile bairdiids (Maddocks 1969, 1976).

The late Tertiary bythocypridids of the Port Phillip and Western Port Basins have undivided or only weakly divided primary adductor muscle scars. This feature distinguishes these forms from the reniform bairdiids belonging to *Papillatabairdia*, adults of which possess eight primary adductor muscle scars (Bentley 1981, Warne, 1986, 1989). *Orlovibairdia mooraboolensis* sp. nov. is the only species described here that possesses both rimmed and unrimmed open normal pore canals. The other species have only unrimmed open normal pore canals.

Subfamily BYTHOCYPRIDINAE Maddocks,
1969

Genus *Bythocypris* Brady, 1880
Subgenus *Bythocypris* (*Bythocypris*) Brady,
1880

Type species. Bythocypris reniformis Brady, 1880.

Remarks. The four species here assigned to *Bythocypris* (*Bythocypris*) have smooth, reniform to subreniform or subrectangular carapaces of varying thickness, inner lamellae of moderate size, adductor muscle scars that are usually undivided, and no marginal denticula-

tion. Their carapaces are narrow in dorsal view but, unlike species of *Anchistrocheles* s.s., are not strongly differentially compressed or flattened along a narrow zone adjacent to the anteroventral and posteroventral margins. The reniform carapace of the type species, *B. (B.) reniformis*, is intermediate in shape between the subrectangular carapace of *B. (B.) subrectangulata* sp. nov. and the subtriangular carapace of *B. (Bythotriangularia)* subgen. nov. Thus, *B. (B.) reniformis* is not indicative of the maximum divergence in lateral outline between *B. (Bythocypris)* and *B. (Bythotriangularia)* but is closer to the subrectangular forms than to the subtriangular forms. Based on Maddocks' (1969, 1973) drawings of *B. (Bythotriangularia)* species, forms assigned to this new subgenus may also have a greater propensity for secondary adductor muscle scar division than species of *Bythocypris* s.s.

Species such as *Anchistrocheles antemacella* Maddocks, 1969, *A. barnharti* Maddocks, 1976, *A. bradyi* Scott, 1905, *A. hartmanni* Maddocks, 1976, *A. mcquadei* Maddocks, 1976, *Anchistrocheles* sp. Whatley & Downing, 1983 and *Cythere acerosa* Brady, 1868 more closely resemble *Bythocypris* s.s. than *Anchistrocheles* s.s. in lateral outline. For example, *A. bradyi* is closer in overall carapace morphology to *Bythocypris* (*Bythocypris*) *subrectangulata* sp. nov. than it is to any species of *Anchistrocheles*, as the latter is here defined. Consequently, the seven species listed above are tentatively transferred to *Bythocypris* (*Bythocypris*), even though they may ultimately warrant new generic or subgeneric status. These species possess slightly more compressed carapaces than many *Bythocypris* (*Bythocypris*) species. Unlike *Anchistrocheles*, however, this compression is not restricted to a narrow zone adjacent to the anteroventral and posteroventral margins but extends over a broader area of the carapace, frequently giving the entire anterior region a flattened, slightly extended appearance. It is not known whether this difference in the type of surface compression corresponds to any consistent differences in soft part anatomy.

Forms such as *Bythocypris* (*Bythocypris*) *bradyi* appear to be transitional in carapace morphology towards deeper water species belonging to *Zabythocypris*, which have very compressed carapaces in dorsal view. This inferred relationship is supported by the tendency of some anteriorly flattened *Bythocypris* (*Bythocypris*) species to develop increased dorsal overlap. In *Zabythocypris*, greatly increased dorsal overlap

has resulted in left and right valves with markedly different length/height ratios.

Of the bythocypridid species in the late Tertiary of the Port Phillip and Western Port Basins, *Bythocypris* (*Bythocypris*) *subrectangulata* is mainly a shallow water species, although it is rare in near-shore facies. *B.* (*Bythocypris*) cf. *affinis*, *B.* (*Bythocypris*) sp. A and *B.* (*Bythocypris*) sp. B occur mainly in deeper water facies (Warne 1987).

***Bythocypris* (*Bythocypris*) *subrectangulata*
sp. nov.**

Figs 1A, 2A–B

Bythocypris sp.—Whitley & Downing 1983: 352, pl. 1, fig. 9.

Bythocypris sp. 1.—Warne 1987: 441.

Etymology. A reference to the subrectangular lateral outline of the carapace.

Holotype. Adult LV, female, NMV P122202, from 1 m above the base of the Fyansford Formation (Early Miocene, late Batesfordian) in the south-west face of Batesford Limestone Quarry, near Fyansford, Victoria (below the upper limit of *Lepidocyclina*); 38°06'S, 144°17'E.

Paratype. Adult RV, male, NMV P122203.

Additional material. Fifty-five mainly disarticulated valves from the Fyansford and Sherwood Formations.

Dimensions. Holotype, LV, female, NMV P122202: L = 1.11 mm, H = 0.59 mm. Paratype, RV, male, NMV P122203: L = 1.09 mm, H = 0.45 mm.

Diagnosis. Carapace moderately large, narrow and subrectangular, of medium shell thickness.

Description. Carapace smooth, moderately robust for family, narrow in dorsal view but without differential compression along marginal regions of lateral surface. Margins of both valves gently rounded and convex, except ventral margins which are concave. Maximum length well below mid-height; maximum height at mid-length; maximum width at mid-length and slightly below mid-height. Posterior slightly more produced and narrower than anterior in RV, less so in LV. Normal pore canals simple, scattered and without rims. Inner lamellae moderately wide; vestibula larger in anterior than posterior; marginal pore canals numerous and straight. Hinge long, simple and adont. Adductor muscle scar pattern consisting of three generally undivided, elongate anterior scars plus one posteroventral scar; middle one of the three

anterior scars sometimes sutured. Mandibular muscle scar pattern consisting of two very narrow scars. Frontal muscle scar pattern consisting of one scar above and slightly anterior to mandibular muscle scar pattern. Various dorsal muscle scars also visible. Sexual dimorphism pronounced, males being more elongate than females.

Remarks. This species is similar in lateral outline to *Bythocypris* (*Bythocypris*?) *bradyi* (Scott, 1905). Although Maddocks (1969) recorded a range of sizes for *B.* (*B.*) *bradyi*, *B.* (*B.*) *subrectangulata* is distinctly larger and not as flattened or produced in the anterior region. In addition, *B.* (*B.*) *bradyi* has slightly broader inner lamellae, a more symmetrically rounded posterior margin, a higher position of maximum length, and a thinner shell. *B.* (*B.*) *reniformis* Brady, 1880 is not as elongated as *B.* (*B.*) *subrectangulata* and has more acutely rounded anterior and posterior margins. The new species is assigned to *Bythocypris* s.s. on the basis of its subrectangular lateral outline and lack of differential compression adjacent to the anteroventral and posteroventral margins.

Age and stratigraphical range. Late Early to early Middle Miocene (Batesfordian to early Bairnsdalian, foraminiferal zones N8–N10/11), in clays and marls of the Fyansford and Sherwood Formations, as well as in calcilutites of the Sherwood Formation.

***Bythocypris* (*Bythocypris*) cf. *affinis*
(Brady, 1886)**

Figs 1B, 2C–D

Bythocypris sp. 3.—Warne 1987: 441.

Anchistrocheles sp. 1.—Warne 1987: 441.

Material. Eight disarticulated adult and juvenile valves from the Fyansford and Sherwood Formations.

Dimensions. LV, female, NMV P122204: L = 1.09 mm, H = 0.55 mm. RV, male, NMV P122205: L = 1.07 mm, H = 0.47 mm.

Description. Carapace elongate, of medium size and thickness for family; LV larger than RV. Overlap greatest in mid-ventral and antero-dorsal regions. Anterior margins of both valves symmetrically rounded, with extremities at mid-height; posterior margins more acutely and asymmetrically rounded, with extremities well below mid-height. Dorsal margins of both valves gently arched, becoming straight anterodorsally;

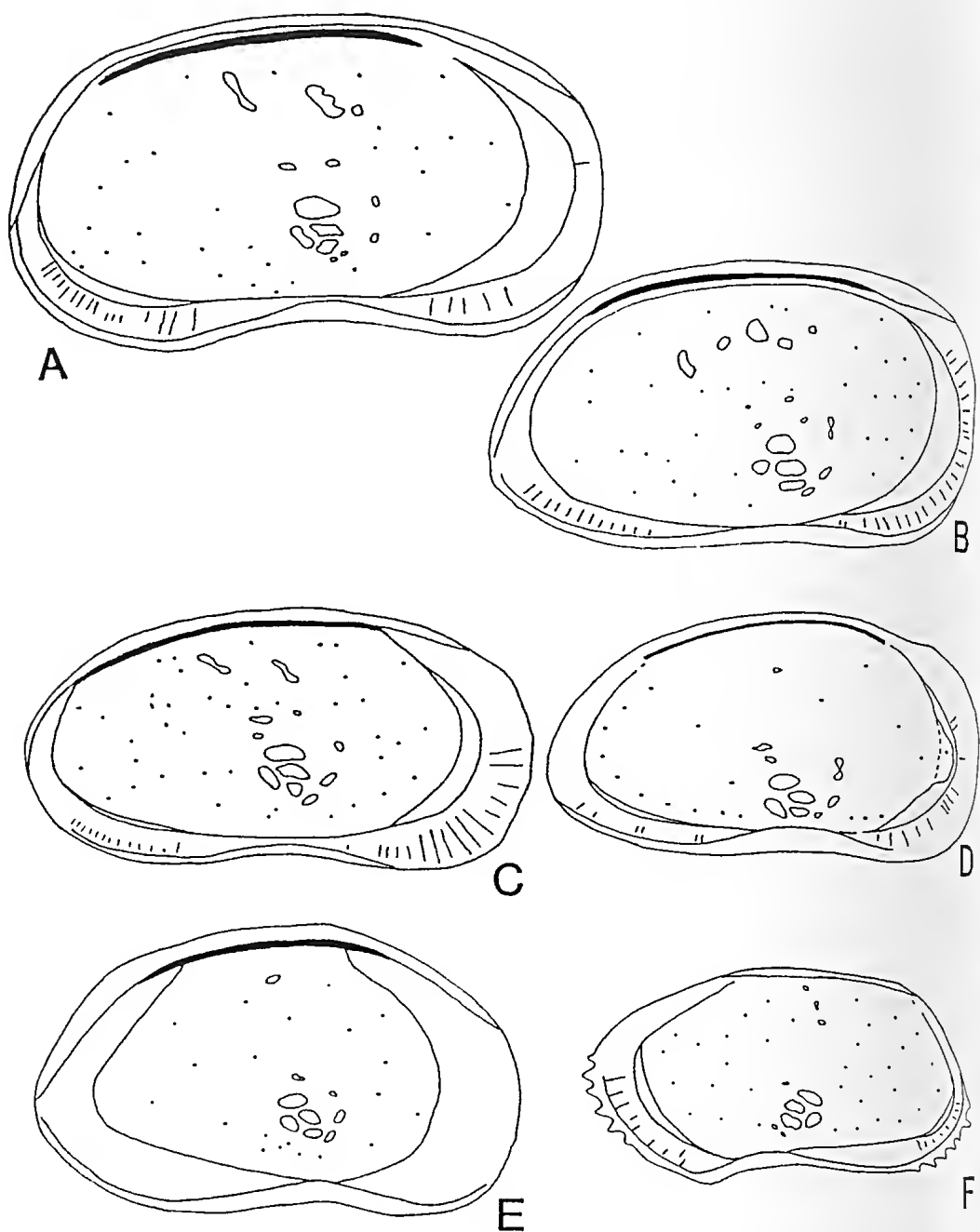


Fig 1. A, *Bythocypris* (*Bythocypris*) *subrectangulata* sp. nov., LV internal, NMV P122202, holotype, female, $\times 71$. B, *Bythocypris* (*Bythocypris*) cf. *affinis* (Brady, 1886), LV internal, NMV P122204, female, $\times 68$. C, *Bythocypris* (*Bythocypris*) sp. A, LV internal, NMV P122206, female?, $\times 85$. D, *Bythocypris* (*Bythocypris*) sp. B, LV internal, NMV P122208, $\times 79$. E, *Anchistrocheles praebensoni* sp. nov., LV internal, NMV P122209, holotype, female, $\times 88$. F, *Orlovibairdia mooraboolensis* sp. nov., RV internal, NMV P122212, paratype, male, $\times 92$. A from Fyansford Formation (late Batesfordian), Batesford Limestone Quarry; B, D-F from Fyansford Formation (Balcombian), Batesford Limestone Quarry; C from Fyansford Formation (Balcombian), Fossil Beach, Mornington.

ventral margins gently concave. Maximum length below mid-height, maximum height at mid-length, and maximum width below mid-height and approximately at mid-length. Valves slightly narrower anteriorly than posteriorly in dorsal view. Normal pore canals simple, scattered and without rims. Inner lamellae wide anteriorly and narrow posteriorly, both with vestibula developed. Marginal pore canals (as seen in anterior part of carapace) scattered and straight. Hinge long, simple and adont. Adductor muscle scar pattern consisting of three generally undivided, irregularly rounded anterior scars plus one similarly shaped posteroventral scar. Mandibular muscle scar pattern consisting of two elongate scars. Frontal muscle scar pattern consisting of two semi-detached oval scars. Dorsal scars visible. Sexual dimorphism evident, males being more elongate than females.

Remarks. This species is similar in size, shape and muscle scar arrangement to various subspecies and variants of *Bythocypris affinis* illustrated by Maddocks (1969), but they all have less acutely rounded posterior margins. *Bythocypris* (*Bythocypris*?) sp. (Whatley & Downing, 1983) [= *Anchistrocheles* sp. Whatley & Downing, 1983] and *B. (B?) antemacella* Maddocks, 1969 are also similar but are smaller, thinner shelled, more asymmetrically and less acutely rounded posteriorly, and slightly more flattened and produced anteriorly. The possibility that the form illustrated here is an intraspecific variant of *B. (B?)* sp. (Whatley & Downing, 1983) is not excluded. Previously (Warne 1987), I assigned specimens of the present form to two different genera on account of the unusually pronounced sexual dimorphism.

Age and stratigraphical range. Early Middle Miocene (Balcombian to early Bairnsdalian, foraminiferal zones N8/9–N10/11), in clays and marls of the Fyansford and Sherwood Formations.

Bythocypris (*Bythocypris*) sp. A

Figs 1C, 2G–H

Bythocypris sp. 2.—Warne 1987: 441.

Material. Thirty-six disarticulated adult(?) and juvenile valves from the Fyansford and Sherwood Formations.

Dimensions. LV, female?, NMV P122206: L = 0.79 mm, H = 0.44 mm. RV, male?, NMV P122207: L = 0.80 mm, H = 0.35 mm.

Remarks. This form is very similar to *Bythocypris* (*Bythocypris*) *subrectangulata* in the shape and clustering of the muscle scars but is smaller, more acutely rounded posteriorly, and has a higher posterior extremity and a greater height to length ratio. The differences in shape are approximately the same if *B. (B.)* sp. A is compared with similar sized juvenile specimens of *B. (B.) subrectangulata*. Furthermore, the inner lamellae in juveniles of *B. (B.) subrectangulata* are narrower and are usually uncalcified. *B. (B.)* sp. A is most abundant in deeper water units of the Fyansford Formation at Mornington, whereas autochthonous occurrences of *B. (B.) subrectangulata* are restricted to the shallow water units of the Fyansford Formation at the Batesford Limestone Quarry (Warne 1987).

Maddocks (1969) noted that some bairdiacean species have the capacity to develop calcified inner lamellae in juvenile stages. It is possible, therefore, that the differences in carapace features between *Bythocypris* (*Bythocypris*) *subrectangulata* and *B. (B.)* sp. A merely reflect ecophenotypic variation within a single species.

Age and stratigraphical range. Early Middle Miocene (Balcombian to early Bairnsdalian, foraminiferal zones N8/9–N10/11), in clays and marls of the Fyansford and Sherwood Formations.

Bythocypris (*Bythocypris*) sp. B

Figs 1D, 2I

Bythocypris sp. 4.—Warne 1987: 441.

Material. One LV from the Fyansford Formation.

Dimensions. LV, NMV P122208: L = 0.87 mm, H = 0.41 mm.

Remarks. This specimen is similar in shape and height/length ratio to *Bythocypris* (*Bythocypris*) *prolata* Maddocks, 1969 but is smaller than adults of that species.

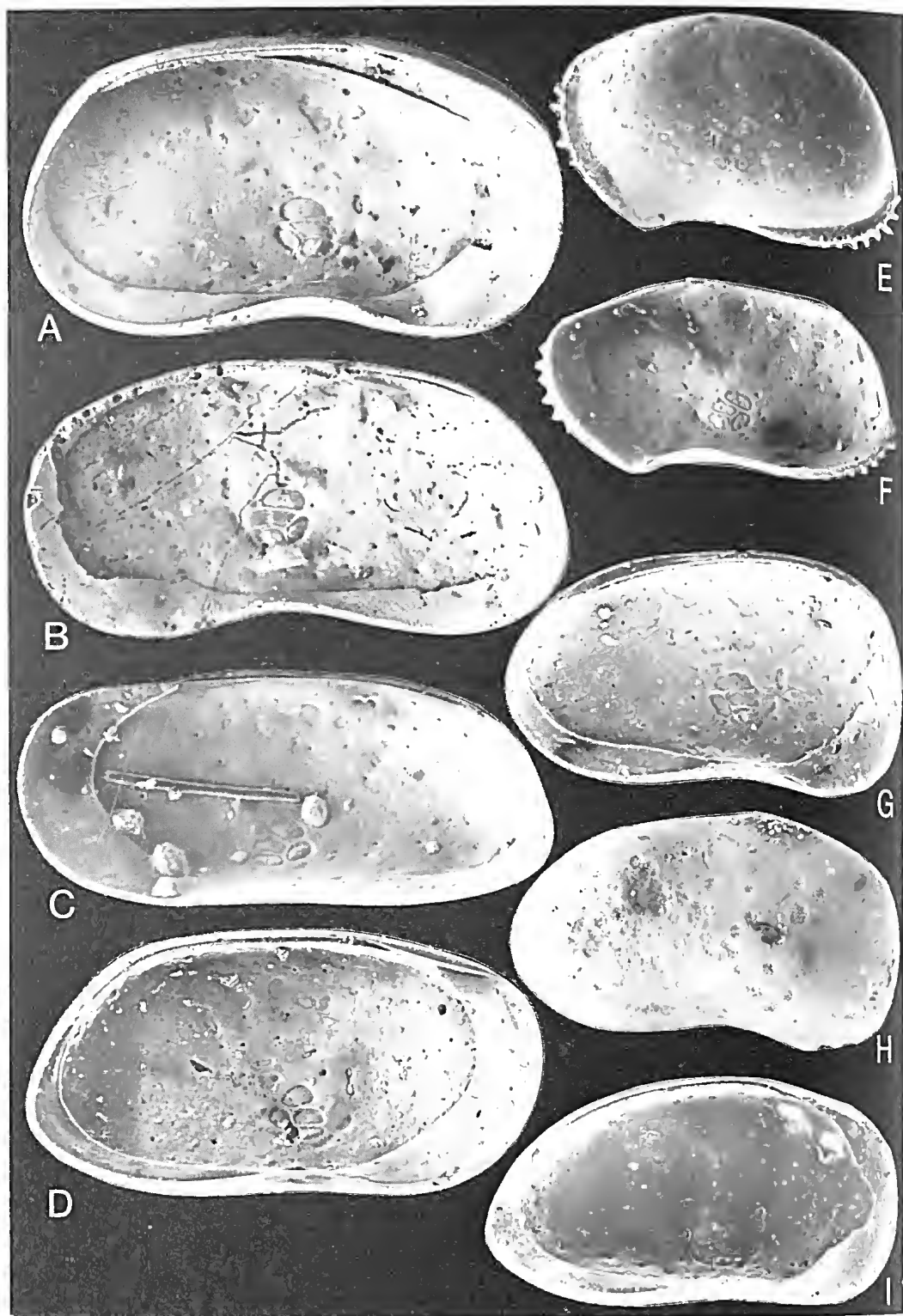
Age and stratigraphical range. Early Middle Miocene (Balcombian, foraminiferal zones N8/9), in clays of the Fyansford Formation.

Subgenus *Bythocypris* (*Bythotriangularia*) subgen. nov.

Etymology. A reference to the family Bythocyprididae and to the subtriangular carapace.

Type species. *Bythocypris spiriscutica* Maddocks, 1969: 96–99, figs 49E–I, 50A–D, 51A–E.

Other species. *B. (Bythotriangularia) eltanina* (Maddocks, 1969); *B. (Bythotriangularia) mozambiquensis*



(Maddocks, 1969); *B. (Bythotriangularia) promoza* (Maddocks, 1973).

Diagnosis. Carapace of medium size, inflated in dorsal view, subtriangular to oval in lateral view and with a strong anterior-posterior asymmetry. Inner lamellae moderately broad; adductor muscle scar pattern typically bythocypridid except that individual scars are commonly divided.

Remarks. The subtriangular to oval carapace distinguishes *B. (Bythotriangularia)* from the more elongated, reniform to subreniform or subrectangular carapace of *B. (Bythocypris)*. Although differences in soft part anatomy are unknown, the shape of the carapace is sufficiently distinct to warrant the recognition of *B. (Bythotriangularia)* as a separate taxon, especially given the small differences in lateral carapace outline between other closely allied bythocypridid genera, such as *Anchistrocheles* s.s. and *Orlovibairdia* s.s. The lateral outline of *B. (Bythotriangularia)* is similar to that of some pontocypridids but they can be easily distinguished by their markedly different adductor muscle scar patterns.

Bythocypris elongata Brady, 1880 may also belong to *B. (Bythotriangularia)* but it is more elongated than the other species included in the new subgenus and has a very narrow inner margin. Teeter (1975) placed *B. elongata* in his new genus *Triangulocypris*, which he regarded as a bythocypridid. His description and illustrations of the adductor muscle scar pattern suggest, however, that *Triangulocypris* belongs to the Paracyprididae, and the genus was assigned to that family by van den Bold (1988). Consequently, *B. elongata* probably does not belong to *Triangulocypris*.

Subfamily PUSSELLINAE Danielopol in Maddocks, 1976

Remarks. The subfamily name dates from Maddocks (1976), the earlier name Pussellidae Danielopol, 1973 being unavailable because the type genus was a *nomen nudum*.

Genus *Anchistrocheles* Brady & Norman, 1889

Type species. *Anchistrocheles fumata* Brady, 1890.

Remarks. *Anchistrocheles* s.s. is here considered to include forms with a reniform to subreniform lateral outline, conspicuous differential compression along a narrow zone adjacent to the anterior, posterior and ventral margins of the lateral surface, and a very broad inner lamella evident except in a relatively small region adjacent to the middle portion of the dorsal margin. *Anchistrocheles* s.s. differs from the deep water *Zabythocypris* in being larger, more robust and significantly less compressed in the middle of the carapace. It differs from *Orlovibairdia* s.s. in lacking marginal spinosity and in having slightly broader inner lamellae.

A variety of forms with differing carapace features have been included in *Anchistrocheles*. One such group includes *A. aculeata* Müller, 1908, *A. aff. aculeata* of Maddocks (1969) and *A. sp. A* Cronin, 1983. These forms, which are here assigned to the new genus *Bythopussella*, may be more closely related to the Caribbean interstitial genus *Pussella* Danielopol, 1976 than to *Anchistrocheles* s.s. Another species group that was erroneously included in *Anchistrocheles* has already been discussed in the remarks on *Bythocypris (Bythocypris)*.

Anchistrocheles praebensoni sp. nov.

Figs 1E, 3A–B

Anchistrocheles sp. 2.—Warne 1987: 441.

Etymology. A reference to the similarity of this species to *Anchistrocheles bensoni* Maddocks, 1969.

Holotype. Adult LV, female, NMV P122209 from near the top of the Fyansford Formation (Middle Miocene, Balcombian) in the south-west face of Batesford Limestone Quarry near Fyansford, Victoria (base of upper quarry bench well above the upper limit of *Lepidocyclina* sp., approximately 25 m above boundary with Batesford Limestone); 38°06'S, 144°17'E.

Paratype. Adult RV, male, NMV P122210.

- * Fig. 2. A, B, *Bythocypris (Bythocypris) subrectangulata* sp. nov. A, LV internal, NMV P122202, holotype, female, × 71. B, RV internal, NMV P122203, paratype, male, × 76. C, D, *Bythocypris (Bythocypris)* cf. *affinis* (Brady, 1886). C, RV internal, NMV P122205, male, × 71. D, LV internal, NMV P122204, female, × 78. E, F, *Orlovibairdia mooraboolensis* sp. nov. E, LV external, NMV P122211, holotype, female, × 89. F, RV internal, NMV P122212, paratype, male, × 90. G, H, *Bythocypris (Bythocypris)* sp. A. G, LV internal, NMV P122206, female?, × 85. H, RV external, NMV P122207, male?, × 81. I, *Bythocypris (Bythocypris)* sp. B, LV internal, NMV P122208, × 78. A, B from Fyansford Formation (late Batesfordian), Batesford Limestone Quarry; C–F, I from Fyansford Formation (Balcombian), Batesford Limestone Quarry; G, H from Fyansford Formation (Balcombian), Fossil Beach, Mornington.

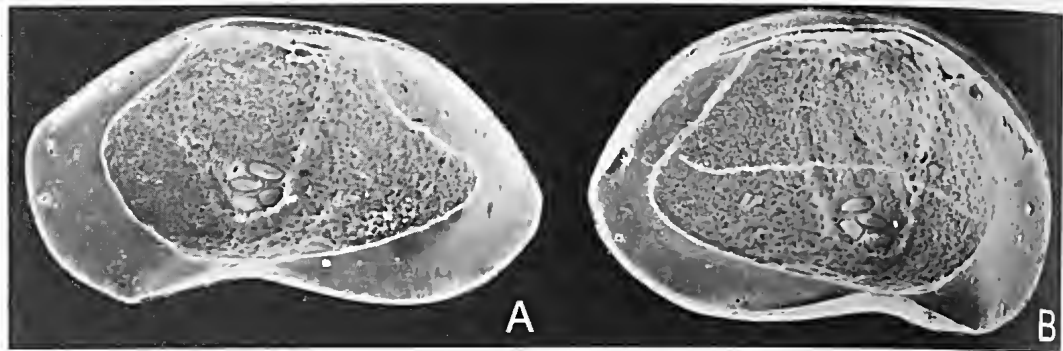


Fig 3. A, B, *Anchistrocheles praebensoni* sp. nov., Fyansford Formation (Balcombian), Batesford Limestone Quarry. A, RV internal, NMV P122210, paratype, male, $\times 86$. B, LV internal, NMV P122209, holotype, female, $\times 90$.

Additional material. Fifty-one articulated and disarticulated adult and juvenile valves from the Batesford Limestone and Fyansford and Sherwood Formations.

Dimensions. Holotype, LV, female, NMV P122209: L = 0.73 mm, H = 0.41 mm. Paratype, RV, male, NMV P122210: L = 0.74 mm, H = 0.34 mm.

Diagnosis. Carapace of varying shell thickness, with narrow, differentially compressed zone adjacent to anteroventral and posteroventral margins; very broad inner lamella evident in all but a relatively small region adjacent to mid-dorsal margin.

Description. Carapace of moderate size, smooth. Most adult specimens of medium shell thickness (opaque), but rare adults and most juveniles with thinner shells (translucent). LV larger than RV and strongly overlapping it. LV asymmetrically rounded anteriorly, with convex anterodorsal and anteroventral margins; extremity at mid-height. Posteriorly, LV more acutely rounded with convex posterodorsal and posteroventral margins; extremity below mid-height. RV similar to LV anteriorly and posteriorly but with straight anterodorsal margin and anterior extremity slightly above mid-height. Ventral margins of both valves strongly incurved. Dorsal margin gently arched in LV, straight in RV. Maximum length below mid-height; maximum height slightly anterior to mid-length. Normal pore canals simple, without rims. Inner lamellae with inner and outer margins not parallel. Inner margin sinuosity as follows. 1. Anterodorsal part of inner margin more or less straight in both valves except near its dorsal margin terminus where it arches slightly towards valve perimeter.

2. Anteroventral part of inner margin gently and evenly arching towards valve perimeter. 3. Anterior section of inner margin approximately parallel to outer margin. 4. Ventral and posteroventral parts of inner margin with no distinct change in curvature between them; they are straight in LV and slightly arched towards ventral perimeter in RV, except posteriorly where they become more strongly arched as part of the acutely rounded posterior extremity of the inner margin. 5. Posterodorsal part of inner margin more or less straight in LV, broadly arched towards centre of carapace in RV. 6. Ventral and posterior sections of inner margin not parallel to outer margin. Vestibula distinct but relatively small. Marginal pore canals abundant and straight. Hinge short and adont. Adductor muscle scar pattern comprising four undivided and unsutured elliptical scars in a loosely packed aggregate. Outer lamellae granular internally in thicker-shelled adults, smooth in thinner-shelled adults and in juveniles. Sexual dimorphism evident, males more elongate than females.

Remarks. *Anchistrocheles praebensoni* sp. nov., *A. bensoni* Maddocks, 1969 and *A. fumata* Brady, 1890 are very similar morphologically, and are here considered to define the morphological limits of *Anchistrocheles* s.s. The three species can be distinguished from each other by their different lateral outlines and by the size and sinuosity of the inner margin.

Specimens identified by Yassini & Jones (1987) as *Bythocypris reniformis* Brady, 1880 are very similar in shape to that species but differ in being differentially compressed along a narrow zone adjacent to the anteroventral and postero-

ventral margins. These specimens may belong to *Anchistrocheles*, a view that is supported by the shape and areal extent of the inner lamella which, although less extensive than that of *A. praebensoni*, is similar in size to that of *A. fumata*.

Anchistrocheles praebensoni is restricted to shallow water facies of the Port Phillip and Western Port Basins.

Age and stratigraphical range. Late Early to early Middle Miocene (Batesfordian to Balcombian; foraminiferal zones N7/8–N8/9), in calcarenites, calcilutites and marls of the Batesford Limestone, Fyansford Formation and Sherwood Formation.

Genus *Orlovibairdia* McKenzie, 1978

Type species. *Bythocypris angulata* Brady, 1870.

Remarks. *Orlovibairdia* is very similar to *Anchistrocheles* in carapace morphology, and both genera include forms with a reniform lateral outline. *Orlovibairdia* species tend to be more elongate, however, and the genus as a whole encompasses forms with a broader range in lateral outline, from reniform to subrectangular. *Orlovibairdia* also differs from *Anchistrocheles* in possessing less extensive inner lamellae, strong anteroventral and posteroventral denticulation, and, in some species, coarse punctate ornament.

Some species of *Orlovibairdia* resemble *Pussella* and *Danipussella* in lateral outline, but members of the last two genera have significantly greater length to height ratios.

Orlovibairdia mooraboolensis sp. nov.

Figs 1F, 2E–F

Orlovibairdia sp. 1.—Warne 1987: 441.

Etymology. A reference to the type locality near the Moorabool River at Fyansford, Victoria.

Holotype. Adult LV, female, NMV P122211 from near the middle of the Fyansford Formation (Middle Miocene, Balcombian) in the south-west face of Batesford Limestone Quarry, near Fyansford, Victoria (base of middle quarry bench above the upper limit of *Lepidocyclus* sp., approximately 10 m above the boundary with Batesford Limestone); 38°06'S, 144°17'E.

Paratype. Adult RV, male, NMV P122212.

Additional material. Twenty-five disarticulated adult and juvenile valves from the Fyansford and Sherwood Formations.

Dimensions. Holotype, LV, female, NMV P122211: L = 0.67 mm, H = 0.37 mm. Paratype, RV, male, NMV P122212: L = 0.66 mm, H = 0.31 mm.

Diagnosis. Carapace relatively small, smooth and elongate, with conspicuous differential compression of anteroventral and posteroventral margins which are strongly denticulate.

Description. Carapace thin shelled; anteroventral margin with six denticles; posteroventral margin with nine denticles. LV larger than RV and overlapping it. LV asymmetrically rounded anteriorly, with convex anterodorsal and anteroventral margins; extremity below mid-height. Posteriorly, LV more acutely rounded with convex posterodorsal and posteroventral margins; extremity below mid-height. RV similar to LV anteriorly and posteriorly but with straight anterodorsal margin. Dorsal margin arched in LV, straight in RV. Ventral margins of both valves strongly incurved. Maximum length slightly below mid-height; maximum height at mid-length in LV, anterior of mid-length in RV; maximum width below mid-height and at mid-length. Normal pore canals open, scattered, some with rims. Inner lamellae relatively narrow compared with type species, wider anteriorly and anteroventrally than posteroventrally. Vestibulum evident but small. Marginal pore canals (as seen anteriorly on carapace) scattered and straight. Adductor muscle scar pattern consisting of four subrounded to elongate scars in a loose aggregate; individual scars sometimes complexly sutured but no discrete division observed. Sexual dimorphism pronounced, males being more elongate than females.

Remarks. *Orlovibairdia mooraboolensis* is similar to *O. angulata* but the latter is slightly larger and possesses a scattered punctate ornament. *O. cf. arcaforma* (Swanson, 1979) [species attributed to Swanson by McKenzie 1978 but a *nomen nudum* when cited] differs from the new species in having a subrectangular lateral outline and strong punctate ornament. *O. formosana* Hu, 1981 from the Pliocene to Pleistocene of Taiwan is smooth like *O. mooraboolensis* but has a subrectangular lateral outline and a denticulate anterodorsal margin.

The variation in lateral outline and ornament outlined above in *Orlovibairdia* species illustrates the mosaic of carapace characters within the genus.

Age and stratigraphical range. Early Middle Miocene (Balcombian to early Bairnsdalian; foraminiferal zones N8/9–N10/11), in marls and clays of the Fyansford and Sherwood Formations.

Genus *Bythopussella* gen. nov.

Etymology. A reference to the family Bythocyprididae and to the possible affinity of the new genus with *Pussella*.

Type species. *Anchistrocheles aculeata* Müller, 1908: 101–102, pl. 14, figs 4–7, pl. 15, figs 1–5.

Other species. *B. aff. aculeata* of Maddocks, 1969, *B. sp. A* (Cronin, 1983) [= *Anchistrocheles sp. A* Cronin, 1983].

Diagnosis. Carapace of moderate size for family, subtrapezoid in lateral outline and compressed in dorsal view. Posterior extremity with prominent terminal spine; anterior extremity generally denticulate and sometimes with terminal spine. Carapace smooth or weakly punctate. Dorsal margin arched in LV, slightly concave in RV. Posterodorsal margin slightly convex in RV, more or less straight in LV. Anteroventral and posteroventral margins broadly convex in both valves. Ventral margin straight in RV, slightly concave in LV. Anterior extremity above mid-height and posterior extremity below mid-height in both valves.

Remarks. The three species here assigned to *Bythopussella* were previously included in *Anchistrocheles* but they differ markedly from members of that genus in lateral outline, in the extent of the inner lamella, and in the usual presence of a terminal posterior spine. *Bythopussella* resembles *Pussella* in that species of both genera may possess a terminal posterior spine. *Bythopussella* differs from *Pussella* and *Daniopussella* in being less elongate. *Bythopussella* is easily distinguished from *Bythotriangularia*, which has a carapace that is subtriangular or oval carapace instead of subtrapezoidal, lacks a posterior terminal spine and is generally more inflated.

The lateral outline of some *Bythopussella* species is perhaps reminiscent of various juvenile bairdiids, some of which also have a posterior terminal spine. Adults of *Bythopussella* differ from juvenile bairdiids, however, in the development of broad inner lamellae and in the overall compression of the carapace.

Bythopussella species appear to inhabit relatively deep marine realms.

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SMALL *POGONA VITTICEPS* (REPTILIA: AGAMIDAE) FROM THE BIG DESERT, VICTORIA, WITH NOTES ON OTHER *POGONA* POPULATIONS

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Adults of *Pogona vitticeps* are smaller towards the southern limit of the distribution of the species, the smallest animals occurring in the Big Desert in western Victoria. Females are not markedly smaller at sexual maturity than males, but males mature at a much smaller size. Data from *P. barbata* suggest that early male maturity in southern areas may occur also in that species. Relative growth and external morphology indicate that the Big Desert population is not taxonomically distinct from *P. vitticeps*. Factors causing the reduced size of animals in the population are unknown.

A POPULATION of *Pogona* lizards from the Big Desert mallee heath in western Victoria has been extensively studied as part of an ongoing project. These lizards closely resemble *P. vitticeps* (Ahl) but are much smaller. *P. vitticeps* typically grows to 250 mm snout-vent length (SVL) (Badham 1976), but the largest specimen collected from the Big Desert is a male of 175 mm SVL (NMV D54760). Morphological features of this population of clearly smaller animals were examined to establish its taxonomic status.

METHODS

Measurements and meristic characters were recorded from museum specimens (see Appendix). Limb, snout-vent and tail lengths were measured to the nearest 0.5 mm using a perspex-mounted ruler. Smaller measurements were taken using dial calipers accurate to 0.05 mm. Where possible, measurements were made bilaterally and the mean used in analysis. Head depth was measured through the centre of the orbit and the maximum head width was also recorded. Other measurements are self-explanatory.

Morphometric data were analysed by calculating the least squares regression for measurements first converted to natural logarithms, allowing the calculation of Huxley's formula for relative growth:

$$Y = bX^a$$

where Y is the measurement under consideration, X the SVL, b a constant and a the allometric coefficient. These regressions were used to calculate theoretical measurements in hatchlings

(45 mm SVL) and in adults near the maximum size of specimens in the Big Desert population (150 mm SVL).

Gonad size and condition were also recorded. Females were considered to be mature if they had oviducal eggs, convoluted opaque oviducts or ovarian follicles more than 5 mm in diameter. Males were assumed to be mature if their testes were enlarged and circular in cross-section. If testicular regression occurs in this species it does not alter the gross appearance of the testes; all males of adult size had apparently mature testes.

Comparisons were made between four groups of specimens: *P. vitticeps* from the Big Desert; *P. vitticeps* from the "Sunset Country" (north-western Victoria north of the Big Desert); *P. vitticeps* from elsewhere (including South Australia, New South Wales, Queensland and the Northern Territory); and *P. barbata*.

RESULTS

Sexual maturity and size

Animals from the Big Desert are clearly smaller than those from the Sunset Country (T-test $P < 0.005$), which are in turn smaller than those from elsewhere ($P < 0.001$) (Table 1).

The smallest Big Desert female with oviducal eggs was 121 mm SVL (NMV D54754), and the smallest female with opaque, convoluted oviducts (indicating previous egg production) was 132 mm SVL (NMV D54051). The largest clearly immature female examined (NMV

Population	N	Mean	Females (SD)	Range	N	Mean	Males (SD)	Range
Big Desert	9	130.8	(13.9)	113–163	11	126.5	(30.2)	83–175
Sunset Country	8	157.5	(28.6)	126–202	6	157.8	(19.4)	131–181
Others	6	184.3	(31.5)	132–217	8	229.0	(16.0)	208–247

Table 1. Size of mature *Pogona vitticeps*.

D55064, 61 mm SVL) has ovarian follicles less than 0.4 mm in diameter. Big Desert females more than 92 mm SVL have ovarian follicles more than 1 mm in diameter. One of these specimens (NMV D54759) has follicles of 6.5 mm diameter and a SVL of 113 mm; this was the smallest female that was clearly mature. Some larger mature females had ovarian follicles of less than 2 mm diameter.

Specimens of *P. vitticeps* from outside the Big Desert mature at a larger size but the difference is not great. A female recorded as coming from "Gawler Ranges, Victoria" (but probably from South Australia; NMV D648) has opaque convoluted oviducts at 128 mm SVL, and a female from near Hattah in northern Victoria was gravid at 126 mm SVL (NMV D11754). Two specimens recorded as coming from Ouyen provide data of dubious significance. One of them (NMV D1031) was clearly immature at 97 mm SVL, having ovarian follicles of less than 1 mm diameter. The other (NMV D970) is only 114 mm SVL yet has opaque convoluted oviducts. Ouyen is north-east of the Big Desert but is the nearest major centre of population east of the desert. The specimens are unlikely to have been collected from the township itself, and either or both of them may have come from the Big Desert or from the Sunset Country. Data from these specimens were excluded from all analyses.

Males from the Big Desert clearly mature at a smaller size than those from elsewhere. One specimen (NMV D18220, 83 mm SVL) has testes approaching 7 mm in length, and another of similar size (NMV D53836, 85 mm SVL) also has larger testes than immature animals (5.6 mm). In comparison, two males of *P. vitticeps* from Purnong in South Australia were immature at SVLs of 88 (NMV D4547; larger testis of 3.15 mm length) and 93 mm (NMV D3072; 4.0 mm). Another specimen from Broken Hill (NMV D52089) was not mature at a SVL of 132 mm, the larger of its testes being only 4.2 mm in length. In these immature specimens the testes are flattened, contrasting sharply with the

swollen, more circular testes of mature animals.

Specimens of *P. barbata* from Victoria are not markedly smaller than those from populations elsewhere. A male from near Boort was 219 mm SVL (NMV D57127). However, a specimen from the south-west of the state (NMV D14699) was a mature male of 95 mm SVL (larger testis 7.45 mm), considerably smaller than the 130 mm stated for mature individuals of both sexes by Badham (1976).

Morphometrics

Data were analysed to quantify allometry in growth. Allometric growth for all populations of *P. vitticeps* is very similar (Table 2). The head of *P. vitticeps* is wider than that of *P. barbata*, especially in larger animals. A clear trend is apparent in the allometric data for head width, populations of larger animals having a higher allometric coefficient. For measurements apart from head width the different *P. vitticeps* populations do not differ substantially. The head is apparently larger in the populations of smaller animals, particularly in juveniles (Table 2).

External morphology

Scale counts and other characters are very similar in specimens of *P. vitticeps* from the Big Desert and from elsewhere (Table 3). A nuchal scale ridge formed by a few mucronate scales with their keels aligned is commonly present in all populations, this ridge continuing well onto the trunk in some animals from the Big Desert population. Individuals from the Big Desert population also commonly possess a paravertebral nuchal scale ridge (about 75% of specimens examined), consisting of a row of mucronate scales parallel to the nuchal scale ridge but a few scales lateral to it. A similar scale row is reported in *P. minimus* (Badham 1976, fig. 4e). Other populations of *P. vitticeps* also commonly possess the paravertebral scale row but the nuchal scale row seldom continues posteriorly.

The venter of the Big Desert animals is commonly patterned in the ocellations typical of

Measurement	Big Desert <i>P. vitticeps</i> (N = 34)				Sunset County <i>P. vitticeps</i> (N = 28)				Other <i>P. vitticeps</i> (N = 31)				<i>P. barbata</i> (N = 35)			
	a	(SE)	X45	X150	a	(SE)	X45	X150	a	(SE)	X45	X150	a	(SE)	X45	X150
Tail	0.97	(0.026)	61.2	196.5	0.87	(0.024)	68.8	197.4	0.89	(0.029)	65.2	191.4	0.99	(0.025)	61.2	201.0
Head width	0.96	(0.029)	11.0	35.1	1.07	(0.034)	10.1	36.4	1.15	(0.038)	9.33	37.1	1.03	(0.035)	9.80	33.8
Snout-parietal	0.70	(0.012)	10.9	25.2	0.69	(0.015)	10.8	24.9	0.69	(0.016)	10.6	24.3	0.72	(0.013)	10.5	24.8
Snout-typanum	0.85	(0.016)	12.4	34.6	0.84	(0.018)	12.2	33.8	0.89	(0.018)	11.5	33.5	0.88	(0.014)	11.7	33.9
Head depth	0.80	(0.027)	8.35	21.8	0.78	(0.019)	8.06	20.6	0.87	(0.020)	7.34	20.9	0.83	(0.023)	7.39	20.0
Tympanum	0.87	(0.040)	1.97	5.65	0.87	(0.031)	1.93	5.49	1.00	(0.045)	1.72	5.72	1.00	(0.025)	1.98	6.65
Hindlimb	0.94	(0.014)	26.6	82.7	0.90	(0.015)	27.9	82.7	0.89	(0.016)	27.6	81.0	0.92	(0.015)	26.3	79.2
Pes length	0.83	(0.016)	11.8	32.3	0.79	(0.017)	12.4	32.1	0.81	(0.023)	11.8	31.1	0.84	(0.020)	11.2	30.9
Forelimb	0.90	(0.017)	19.4	57.5	0.92	(0.017)	19.6	59.4	0.89	(0.018)	20.3	59.3	0.92	(0.016)	19.3	58.2

Table 2. Allometric characters of *Pogona* populations; a = allometric coefficient; X45 = calculated length of the part at a snout-vent length of 45 mm; X150 = similar calculation at SVL of 150 mm.

Count	Big Desert <i>P. vitticeps</i> (N = 34)				Sunset County <i>P. vitticeps</i> (N = 17)				Other <i>P. vitticeps</i> (N = 25)				<i>P. barbata</i> (N = 26)			
	Mean	(SD)	Range	Mean	(SD)	Range	Mean	(SD)	Mean	(SD)	Range	Mean	(SD)	Range	Mean	Range
PNS	4.94	(0.69)	4-6	5.24	(0.90)	4-7	4.64	(0.71)	4.62	(0.64)	3-6	4.62	(0.64)	4-6	4.62	4-6
SNS	4.29	(0.58)	3-6	4.29	(0.77)	3-6	4.52	(0.77)	4.12	(0.65)	3-6	4.12	(0.65)	3-5	4.12	3-5
INS	11.06	(1.2)	8-13	11.29	(1.1)	9-13	10.92	(1.1)	10.31	(1.0)	9-13	10.31	(1.0)	9-13	10.31	9-13
SPS	14.06	(1.1)	12-17	15.24	(1.9)	11-19	15.24	(1.8)	14.48	(1.6)	12-20	14.48	(1.6)	13-18	14.48	13-18
SOS	4.32	(0.47)	4-5	4.53	(0.51)	4-5	4.32	(0.48)	4.35	(0.49)	4-5	4.35	(0.49)	4-5	4.35	4-5
SLS	16.74	(1.1)	15-19	16.68	(1.1)	15-19	17.28	(1.1)	17.0	(1.2)	15-19	17.0	(1.2)	14-19	17.0	14-19
ILS	15.76	(1.2)	14-18	15.94	(1.1)	13-18	16.20	(1.2)	16.2	(1.2)	14-19	16.2	(1.2)	15-18	16.2	15-18
MBS	145.3	(11.8)	129-164	—	—	—	138.2	(10.6)	141.1	(15.6)	119-154	141.1	(15.6)	101-175	141.1	101-175
FPS	15.09	(2.0)	11-19	14.63	(1.5)	12-17	13.80	(2.2)	14.6	(2.1)	9-19	14.6	(2.1)	11-19	14.6	11-19
SDL	21.64	(1.3)	19-25	22.06	(1.1)	20-24	21.60	(2.0)	22.7	(2.0)	18-26	22.7	(2.0)	18-26	22.7	18-26

Table 3. Comparative scale and pore counts; PNS = prenasal scales; SNS = subnasal scales; INS = internasal scales; SPS = scales from rostral to interparietal; SOS = scales from lower border of orbit to supralabial series; SLS = supralabial scales; ILS = infralabial scales; MBS = mid-body scale rows; FPS = femoral pores (total); SDL = number of lamellae under fourth toe.

Pogona species. Badham (1976) reported that the venter of *P. vitticeps* was "rarely patterned except in juveniles". This colour pattern in the Big Desert animals is therefore interpreted as a neotenic character.

Sexual dimorphism

There is little size difference between the sexes (Table 1). Males are a little larger than females, significantly so in the non-Victorian specimens ($P = 0.011$). Limb and tail lengths are relatively greater in males, as noted by Badham (1976), and the head of males is relatively wider.

In Big Desert animals the tympanum alters in shape from almost circular in hatchlings to oval in adults. This change is much more pronounced in females and may be used with reasonable reliability to sex adults. This dimorphism is less pronounced in other *P. vitticeps* populations and is not apparent in *P. barbata*.

DISCUSSION

The broad head of *P. vitticeps* is a characteristic difference from other species of *Pogona* (Badham 1976), and the Big Desert population shares this character. In all head measurements, the calculated juvenile figures (X45, Table 2) for the Big Desert population are higher than those for other populations, but at adult size (X150, Table 2) the differences are negligible. This result is surprising because allometric coefficients are usually more labile than juvenile proportions (Witten 1985), and we can think of no adaptive explanation for it. It is possibly an artifactual result arising from earlier maturation in the Big Desert population.

The differences in scale and pore counts are of a magnitude to be expected from different populations of a single species. Although some differences exist, such as a lower number of scales from rostral to interparietal and a higher number of femoral pores in the Big Desert population, these are not great and fall far short of reasonable diagnostic characters.

The taxonomic status of the population from the Big Desert should remain unchanged. There is no evidence from any character examined which would support the erection of a new taxon to accommodate the population. Accordingly, it

should be recognised as a population of *P. vitticeps* which fails to achieve large size. We have no evidence indicating whether the reduced size of the species in the Victorian mallee is genetic or phenotypic.

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APPENDIX

Specimens examined

All specimens are housed in the Museum of Victoria (NMV) or the Australian Museum (AM).
Big Desert *P. vitticeps*. NMV: D18220, D52637, D52690, D52742, D53482, D53827, D53836, D53853, D53907, D53925, D54051, D54070-1, D54123, D54131-2, D54144, D54557, D54749, D54754, D54759-60, D54789-90, D55036, D55064, D55251, D55305, D55583, D56741, D58501, D58548, D58555, D59448, D59818.
Sunset Country *P. vitticeps*. NMV: D699-700, D11753-4, D15379, D15382, D47858, D58472, D58477, D60324-5, D60609, D60694-5, D60708, D60741, D60760, D60762-3, D60768-9, D60778, D60785, D60826-8, D60841, D60854.
Other *P. vitticeps*. NMV: R4547-8, R13781-2, D1123, D3072, D8970, D12164, D14181, D41501-2, D52088-9, D58570. AM: R13904-5, R15295, R17122-3, R21077, R47319, R107398, R107406, R107409-10, R107444, (Field tags) 11252, 11350, 11358-9.
P. vitticeps not used in analysis. NMV: R4855, D648, D777, D787, D970, D1031, D1036, D7871.
P. barbata. NMV: D137, D151, D723, D744, D896, D966, D1345, D7934, D8038, D14034, D14036, D14679, D14699, D48900, D57127. AM: R17904, R20987, R21578, R25789, R107397, R107399-405, R107407-8, R107411-3, (Field tags) 11347-9, 11360.

SHORT COMMUNICATION

RE-ASSESSMENT OF THE ARABIAN PERMIAN CHONETID BRACHIOPOD
CHONETES ARABICUS HUDSON & SUDBURY

CHONETES ARABICUS is a remarkable tiny species of a chonetid brachiopod originally described from the Early Permian Lusaba Limestone of the Haushi Area (Sultanate of Oman) by Hudson & Sudbury (1959). The small size of the species raises questions as to its correct generic placement, despite the assignment of the species by Archbold (1983: 68) to *Neochonetes* (*Sommeriella*), a subgeneric group noted for its larger species size (Archbold 1981).

The new material described herein permits us to confirm the generic position of the species and to assess several critical morphological characters.

In 1984 one of us (C.F.B.) collected a large suite of topotypic specimens from the Lusaba Limestone. The limestone is interpreted as being a shallow marine deposit from an open subtidal environment with fairly high energy conditions, consistent with the earlier views of Hudson & Sudbury (1959).

The age of the Lusaba Limestone was considered by Hudson & Sudbury (1959) to be comparable with that of the Fossil Cliff Formation of Western Australia (a unit usually considered to be of Sterlitamakian age; Archbold 1982), but, as the Lusaba Limestone occurs stratigraphically above the occurrence of the Late Sakmarian (Sterlitamakian) ammonoid *Metalegoceras*, the formation may be earliest Artinskian (Aktasian) as suggested by Waterhouse (1976: 84).

MORPHOLOGY OF THE SPECIES

The species was well described by Hudson & Sudbury (1959), although some doubt has existed as to whether their material represented a mature species. We illustrate three specimens (Fig. 1A-C), coated with ammonium chloride, to provide details not clearly visible in the original figures of uncoated specimens

Specimen No.	Width	Hinge width	Ventral height	Dorsal height
UTGD 98800	9.8	8.8	—	7.0
UTGD 98799	7.2	6.8	5.5	—
UTGD 98798	6.8	5.8	—	4.5

Table 1. Measurements of figured specimens (in mm).

(Hudson & Sudbury 1959, pl. 3, figs 6-16, pl. 6, figs 14-18).

Measurements of the three figured specimens are provided in Table 1. Specimens are held in the Department of Geology, University of Tasmania. Pertinent morphological features include the distinct brachial ridges of the largest dorsal valve (UTGD 98800), indicating the maturity of the specimen, and the nature of the ventral internal rows of papillae and the dorsal external ornament (UTGD 98799 and 98798 respectively). The coarse denticulation of the ventral hinge reported by Hudson & Sudbury (1959) is regarded by us as due to post mortem abrasion of isolated valves. The feature is variably developed, often irregular, and a similar appearance can occur at the rear margin of the ventral interarea.

We conclude that the species belongs in *Neochonetes* (*Sommeriella*) and that the larger representatives of the species are mature specimens rather than juveniles.

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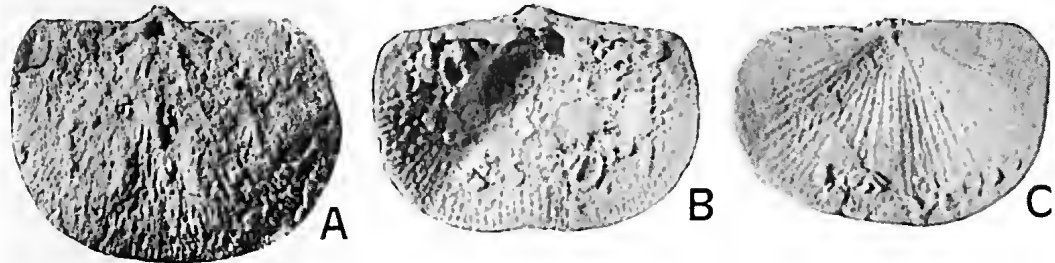


Fig. 1. A-C, *Neochonetes* (*Sommeriella*) *arabicus* (Hudson & Sudbury). A, UTGD 98800, dorsal valve internal view, $\times 5$. B, UTGD 98799, ventral valve internal view, $\times 5.5$. C, UTGD 98798, dorsal valve external view, $\times 5.5$.

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THE ANT FAUNA OF A MALLEE OUTLIER NEAR MELTON, VICTORIA

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Long Forest mallee, near Melton, Victoria, occurs 110 km from the nearest other mallee vegetation and is therefore of considerable biogeographic interest. Ants were sampled directly by hand and by pitfall trapping during 1983-1985, with a total of 77 species from 21 genera recorded. The fauna was dominated by the meat ant, *Iridomyrmex purpureus* (29% of all ants in traps), with species of *Monomorium* (8 species, total of 25% of all ants), *Pheidole* (5 species, 13% of all ants), and *Notoncus "enormis"* (8% of all ants) also abundant. In many respects the fauna resembles that at Wyperfeld National Park located in the major mallee region of northwestern Victoria: many species and species-groups are shared, and the overall biogeographical profiles and composition of functional groups are similar. However, the Long Forest fauna has several important differences which reflect the site's southerly location, including a lower species to genus ratio, a lower representation of Eyrean taxa, a higher abundance of Bassian elements, and the occurrence of some species characteristic of cooler and wetter parts of southern Victoria.

AN ISOLATED outlier of mallee vegetation (hereafter referred to as Long Forest mallee) occurs south of the Great Dividing Range in a rain-shadow area (mean annual rainfall approximately 500 mm) near Melton, 50 km west of Melbourne. It is by far the most southerly patch of mallee in southeastern Australia, occurring 110 km southeast from the nearest similar vegetation at Bendigo. Several plant species found in Long Forest mallee, such as *Rhagodia parabolica* (only found in Victoria in the immediate region), *Sclerolaena diacantha* and *Myoporum deserti*, are characteristic of the arid zone (Myers et al. 1986).

The insect fauna of Long Forest mallee is poorly known but clearly is of considerable biogeographic interest. Here we document the ant fauna of a site within Long Forest mallee and compare it with those of two well-studied sites which represent biogeographic contrasts in Victoria. One of these sites is at Wyperfeld National Park (mean annual rainfall approximately 400 mm) in the major mallee region of semi-arid northwestern Victoria (Andersen 1983, 1984, Andersen & Yen 1985), and the other is Wilsons Promontory (mean annual rainfall 1000-1200 mm) on the southern coast (Andersen 1986a, b, 1988). These sites support contrasting ant faunas. The major elements at Wilsons Promon-

tory are Bassian taxa (Andersen 1991a) such as the *nitidiceps-foetans* complex of *Iridomyrmex*, *Rhytidoponera tasmaniensis*, *R. victoriae*, and species of *Notoncus* and *Prolasius*. Arid-adapted (Eyrean) taxa such as *Melophorus* spp. are poorly represented. A substantial number of Bassian elements are also present at Wyperfeld but they occur within a framework of predominantly arid-adapted taxa, particularly species of *Iridomyrmex*, *Camponotus* and *Melophorus*. These three genera represent the "core" taxa of Australian arid-zone communities, together usually contributing about half the total species (Greenslade 1979, Greenslade & Greenslade 1989).

STUDY SITE

Long Forest mallee is described in detail by Myers et al. (1986). It occupies an area of approximately 1.5 km² (it was three times this size before clearing commenced 25 years ago), and is dominated by the mallee eucalypt *E. behriana* of up to 10 m in height, with a sparse understorey of grasses, perennial herbs and chenopods. The soil is a Tertiary sandy clay. The study was conducted within an area of approximately 1 ha, located in a property owned by Dr and Mrs M. Baker.

METHODS

Ants were sampled between 1983 and 1985 by collecting them directly from the ground and from vegetation, and by pitfall trapping. Pitfall traps were 35 mm diameter plastic vials, partly filled with 70% ethanol, which were buried with their rims flush to the soil surface. Traps were similar to those used at Wilsons Promontory and Wyperfeld, and the catches are likely to provide a good indication of the relative abundance of species on the ground (Andersen 1983, 1986a, 1991b). The traps were arranged in a 5×6 grid with 5 m spacing (area of grid 500 m²), and operated for 4-day periods during January 1983, October 1983 and May 1985. Hand collections were conducted during these periods and also on other occasions covering all seasons. Ant species captured in traps were scored according to a five point abundance scale (1 = 1 ant; 2 = 2–5 ants; 3 = 6–20 ants; 4 = 21–50 ants; 5 = > 50 ants) in order to reduce distortions caused by large numbers of ants falling into a few traps (see Andersen 1991b). These abundance scores were used directly as counts when calculating relative abundances.

Most of the ants collected could not be identified to species with certainty because of our generally poor taxonomic knowledge of Australian ants. Where possible, these species were assigned to informal species-groups (denoted by inverted commas, eg. *Camponotus* "claripes") derived by the senior author from type specimens held in the Museum of Victoria and in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra (see Andersen 1991a). A complete set of voucher specimens is held by the senior author.

In the absence of a published biogeographic treatment of the Australian ant fauna, each species was judged to belong to groups with Bassian, Eyrean or widespread distributions according to the senior author's understanding of Australian ants. The pattern of community organisation was investigated by classifying species into functional groups according to their presumed habitat requirements and competitive interactions. This classification is modified from Greenslade (1978), and has been used extensively in studies of Australian ant communities (see Greenslade & Greenslade 1989, Andersen 1990, 1991c).

The biogeographic profile and pattern of community organisation of the Long Forest mallee fauna was compared with those of Wyperfeld and Wilsons Promontory. The species lists from

these other localities were obtained from detailed studies of small plots, as at Long Forest mallee. The Wilsons Promontory data are from two woodland sites each of approximately 0.25 ha (Andersen 1986a, 1988), and the Wyperfeld data are from adjacent heath and mallee sites each of 0.13 ha (Andersen 1983, 1984, Andersen & Yen 1985).

RESULTS

A total of 77 species from 21 genera were collected (see appendix), with 44 of these caught in traps. The species accumulation curve (Fig. 1) suggests that the number of species occurring in the 500 m² trapping grid was in excess of 50. The richest genera were *Camponotus* (12 species), *Monomorium* (11), *Iridomyrmex* (8), *Myrmecia* (7), *Melophorus* (5) and *Pheidole* (5). The mean number of species per genus was 3.7, midway between that at Wilsons Promontory (2.9) and at Wyperfeld (4.6). *Iridomyrmex*, *Camponotus* and *Melophorus* together contributed 32% of total species at Long Forest mallee, again midway between Wilsons Promontory (23%) and Wyperfeld (42%).

The biogeographic profile of the Long Forest mallee fauna resembles that at Wyperfeld far

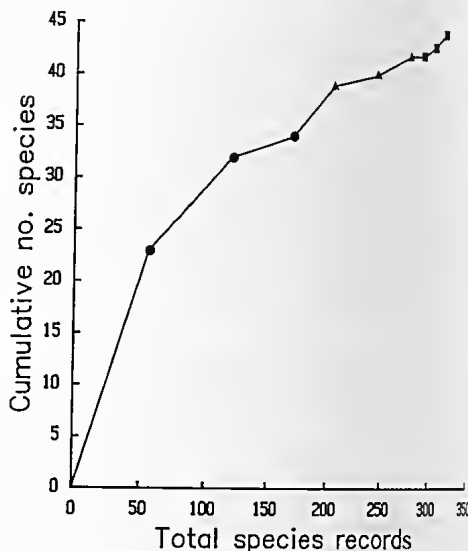


Fig. 1. Accumulation of ant species in pitfall traps (500 m² grid) at Long Forest mallee. Each point represents the running total of ten traps (circles = January 1983; triangles = October 1983; squares = May 1985). Number of species records is the sum of the total number of species recorded in each trap, regardless of species turnover across traps.

	Bassian	Eyrean	Widespread
Long Forest mallee (n = 77)	16	21	64
Wilsons Promontory (n = 83)	37	5	58
Wyperfeld (n = 138)	17	28	55

Table 1. Biogeographical profile of the Long Forest mallee ant fauna (see appendix for biogeographic affinities of individual species) compared with those at Wilsons Promontory (combined lists of Andersen 1986a, 1988) and Wyperfeld (list of Andersen & Yen 1985). Data are the percentages of species having Bassian, Eyrean and widespread distributions.

more than Wilsons Promontory (Table 1). The proportions of Bassian taxa are very similar at the first two locations (16% and 17% respectively, compared with 37% at Wilsons Promontory), with Eyrean taxa being slightly less prominent at Long Forest mallee (21% versus 28%, compared with 5% at Wilsons Promontory). The closer affinities of the Long Forest mallee fauna to that at Wyperfeld is further suggested by the distributions of individual species and species-groups. Of the 35 Long Forest taxa identified at this level, 15 (*Myrmecia* sp. nr *mandibularis*, *M. dichospila*, *M. "nigriceps"*, *M. "tepperi"*, *Mesostroma loweryi*, *Monomorium "insolescens"*, *Podomyrma adelaidae*, *Iridomyrmex "discors"*, *I. "nitidus"*, *I. purpureus*, *Camponotus "ephippium"*, *C. "suffusus"*, *C. "tricoloratus"*, *Notoncus "enormis"* and *Polyrhachis phryne*) occur at Wyperfeld but not Wilsons Promontory, whereas the reverse is true for only five (*Myrmecia urens*, *Rhytidoponera tasmaniensis*, *Monomorium "flavigaster"*, *Tapinoma "minutum"* and *Notoncus "ectatommoides"*). The occurrence of *Myrmecia forceps* at Long Forest mallee appears to be the first record of this species in Victoria (see Clark 1951, Taylor & Brown 1985).

Dominant species of *Iridomyrmex* comprised 31% of all ants captured in pitfall traps at Long Forest mallee (Table 2). *Iridomyrmex purpureus*, a member of the meat ant complex (Greenslade 1976, Greenslade & Halliday 1982), was by far the leading dominant, comprising 29% of total catches (93% of total *Iridomyrmex*). The other major functional group was "generalised Myrmicinae" (mostly species of *Monomorium* and, to a lesser extent, *Pheidole*), which comprised 39% of total catches. "Associated subordinate Camponotinae" (primarily species of *Camponotus*) and "hot and cold climate specialists" contributed many species, but, aside from

Notoncus "enormis" (8% total catches), none were frequently recorded in traps.

Functional group composition at Long Forest mallee is extremely similar to that at Wyperfeld, the correlation (r ; $n = 9$) between percentage abundance sub-totals in Table 2 being 0.97. The only substantial difference is the relatively high abundance of "cold climate specialists" (primarily *N. "enormis"*) at Long Forest mallee (Table 2). However, although the total relative abundance of "generalised Myrmicinae" was similar, species of *Pheidole* and *Monomorium* were respectively more and less prominent at Long Forest mallee. The sub-totals in Table 2 for Wilsons Promontory are not related ($r = -0.17$, $p > 0.05$) to those for Long Forest mallee.

DISCUSSION

The ant fauna of Long Forest mallee is very similar to that at Wyperfeld in terms of its biogeographical profile (Table 1) and functional group composition (Table 2). Many species and species-groups occur at both sites. However, there are several important differences, all of which reflect the Long Forest mallee's higher rainfall and southerly location. The differences are: a lower species to genus ratio; a lower representation of Eyrean taxa (Table 1), particularly *Melophorus* (Table 2); a higher abundance of Bassian elements (*Notoncus*, Table 2); and the occurrence of some species characteristic of cooler and wetter parts of southern Victoria (such as *Rhytidoponera tasmaniensis*). The Long Forest site can therefore be described as supporting an ant fauna essentially typical of the mallee region of northwestern Victoria, but with a somewhat greater Bassian influence.

Several Bassian taxa that occur at Wyperfeld were not recorded at Long Forest mallee. These include *Iridomyrmex "itinerans"* and species of *Dolichoderus* and *Prolasius*. It is possible, however, that these taxa are present locally but outside the study site. A larger number of Eyrean and arid-adapted tropical taxa that occur at Wyperfeld were also not recorded at Long Forest mallee, and many of these probably do not occur there. They include species of *Cerapachys*, *Monomorium* ("*Chelaner*") (eg. "*rothsteini*", "*whitei*"), *Tetramorium*, *Camponotus* (eg. "*aurorincta*", "*whitei*"), *Melophorus* (eg. "*aeneovirens*") and *Opisthopsis*.

The Long Forest site is a mallee ecosystem on Melbourne's doorstep. It has suffered from poor management decisions in the past but is now a

	Long Forest	Wyperfeld	W Prom
1 Dominant Dolichoderinae			
<i>Iridomyrmex</i>	5 (31)	13 (35)	8 (18)
sub-total	5 (31)	15 (35)	8 (18)
2 Associated Subordinate Camponotini			
<i>Camponotus</i>	12 (4)	29 (2)	3 (9)
<i>Polyrhachis</i>	1 (—)	5 (—)	2 (—)
sub-total	13 (4)	34 (2)	5 (9)
3a Hot Climate Specialists			
<i>Meranoplus</i>	10 (2)	3 (1)	0
<i>Monomorium</i> ("Chelaner")	2 (—)	4 (—)	0
<i>Podomyrma</i>	1 (—)	1 (—)	0
<i>Melophorus</i>	5 (—)	13 (8)	0
sub-total	18 (3)	22 (9)	0
3b Cold Climate Specialists			
<i>Epopostruma</i>	1 (—)	2 (—)	0
<i>Mesostruma</i>	1 (—)	1 (—)	0
<i>Monomorium</i> ("Chelaner")	1 (—)	0	4 (4)
<i>Podomyrma</i>	1 (—)	2 (—)	1 (—)
<i>Myrmecorhynchus</i>	1 (—)	0	0
<i>Notoncus</i>	3 (8)	3 (—)	1 (10)
sub-total	8 (8)	15 (—)	9 (14)
4a Cryptic Species			
<i>Hypoponera</i>	1 (—)	0	1 (—)
<i>Solenopsis</i>	2 (1)	1 (—)	1 (14)
sub-total	3 (1)	4 (—)	3 (14)
4b Sub-cryptic Species			
<i>Iridomyrmex</i> "darwinianus"	2 (3)	1 (9)	0
<i>I.</i> "glaber"	1 (1)	2 (—)	0
<i>Tapinoma</i>	1 (—)	0	1 (—)
<i>Paratrechina</i> "minutula"	1 (7)	1 (—)	1 (—)
<i>Stigmatopora</i>	2 (2)	13 (2)	3 (—)
sub-total	7 (13)	17 (11)	6 (5)
5 Opportunists			
<i>Rhytidoponera</i>	1 (1)	0	2 (27)
sub-total	1 (1)	5 (—)	3 (37)
6 Generalised Myrmicinae			
<i>Crematogaster</i>	1 (1)	6 (3)	1 (—)
<i>Monomorium</i>	8 (25)	8 (35)	1 (—)
<i>Pheidole</i>	5 (13)	6 (4)	4 (1)
sub-total	14 (39)	22 (42)	6 (1)
7 Large, Solitary Foragers			
<i>Myrmecia</i>	7 (—)	4 (—)	5 (2)
<i>Trachymesopus</i>	1 (—)	0	0
sub-total	8 (—)	4 (—)	6 (2)
Total	77 (100)	138 (100)	47 (100)

Table 2. Ant community organisation at Long Forest mallee compared with that at Wyperfeld (combined heath and mallee plots, data from Andersen 1983, Andersen & Yen 1985) and Wilsons Promontory (data from woodland site in Andersen 1986a). Taxa are classified into functional groups according to their habitat requirements and competitive interactions (see text). Data are numbers of species per taxon and, in brackets, their percentage abundance in pitfall traps (dashes indicate less than 1%).

Victorian National Parks and Wildlife Service Reserve. Its unique biogeography make it a significant part of Victoria's natural heritage.

ACKNOWLEDGEMENTS

We are most grateful to Dr and Mrs Baker for allowing us to work on their property, and for their efforts in protecting what remains of Long Forest mallee. Dr J. D. Majer and two anonymous referees made valuable comments on the draft manuscript. This is TERC library contribution no. 677.

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APPENDIX

List of ant species recorded at Long Forest mallee. Authorities for species names are given in Taylor & Brown (1985). The biogeographical affinity of each species (B = Bassian, E = Eyrean, W = widespread) is also given.

MYRMECINAE

Myrmecia (*tepperi* gp) *dixonii* (W)
M. (nigriceps) gp fasciata (W)
M. forceps (W)
M. (urens) gp ?dichospila (W)
M. pyriformis (W)
M. urens (W)
M. (mandibularis) gp sp. (W)

PONERINAE

Hypoponera sp. (W)
Rhytidoponera tasmaniensis (B)
Trachymesopus rufoniger (B)

MYRMICINAE

Crematogaster sp. (W)
Epopostruma "quadrspinosa" (B)

Meranoplus spp. ($\times 10$; W)
Mesostruma loweryi (B)
Monomorium ("Chelaner") "insolescens" (2 spp.; E)
M. ("Chelaner") "flavigaster" (B)
Monomorium spp. ($\times 8$; W)
Pheidole spp. ($\times 5$; W)
Podomyrma adelaidae (B)
P. ?*rugosa* (B)
Solenopsis spp. ($\times 2$; W)

DOLICHODERINAE

Iridomyrmex "bicknelli" (E)
I. "darwinianus" (2 spp.; W)
I. "discors" (E)
I. "glaber" (W)
I. "gracilis" (E)
I. "nitidus" (W)
I. *purpureus* (E)
Tapinoma "minutum" (W)

FORMICINAE

Camponotus (*suffusus* gp) *bendigenis* (E)
C. "claripes" (3 spp.; W)
C. (*consobrinus-nigriceps* gp) *obniger* (W)
C. "ephippium" (2 spp.; E)
C. "nigroaeneus" (2 spp.; W)
C. "rubiginosus" (W)
C. "tricoloratus" (E)
C. *suffusus* (E)
Melophorus "hirsutus" (E)
Melophorus spp. ($\times 4$; E)
Myrmecorhynchus "emeryi" (B)
Notoncus "ectatommoides" (B)
N. "enormis" (B)
N. "hickmani" (B)
Paratrechina "minutula" (W)
Polyrhachis *plurys* (B)
Stigmacros ("Campostigmacros") sp. (W)
S. ("Stigmacros") sp. (W)

THE BEALIBA METEORITE FROM VICTORIA

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BIRCH, W. D., 1991:06:30. The Bealiba Meteorite from Victoria. *Proceedings of the Royal Society of Victoria* 103 (1): 7–11. ISSN 0035-9211.

The Bealiba Meteorite is an L6 chondrite discovered in the collections of the Geological Survey of Victoria. The single 652 gram specimen was donated to the Geological Survey in 1950 by J. E. Renshaw but was not recognised as a meteorite. The collecting site was given as "one mile north of Bealiba", Victoria. The meteorite consists of poorly defined chondrules and irregular metallic grains in a recrystallised matrix. The main minerals present are orthopyroxene, olivine, oligoclase, troilite, kamacite, taenite, diopside and chromite. Microprobe analyses of these minerals are typical of L6 chondrites. Goethite alteration occurs around the Fe-Ni grains and in veinlets in the groundmass. The Bealiba Meteorite is the second L6 chondrite discovered in Victoria.

THE BEALIBA meteorite is a previously unrecorded L6 chondrite, with a fall site near the small central Victorian town of Bealiba (36°48' S, 143°33' E), about 30 km northwest of Maryborough (Fig. 1). The specimen was discovered during early 1989 in the collections of the Geological Survey of Victoria (GSV), following their transfer to the Museum of Victoria in 1987. The author recognised the meteorite while sorting a tray of miscellaneous rocks. It was registered in the GSV collection as no. 11635 and labelled as "ironstone with sandstone", from 1 mile north of Bealiba, Victoria. It had been donated to the GSV by Mr J. Renshaw in October 1950. The Bealiba meteorite is now registered as no. E12275 in the collection of the Department of

Mineralogy and Petrology, Museum of Victoria. The name, together with data for classification, were approved by the Nomenclature Committee of the Meteoritical Society early in 1990.

HISTORY OF DISCOVERY

In order to verify the original fall site, attempts were made to contact surviving members of the Renshaw family. Two sisters, Alva and Mary Renshaw, of Newstead, Victoria, confirmed that their late brother, Joseph E. Renshaw (1907–1977), was an avid collector of geological specimens and spent considerable time fossicking in bushland around Bealiba. He also paid regular visits to the GSV Museum in Melbourne. The father of the family, Joseph A. Renshaw, ran a drapery in Bealiba and owned a 10-acre "paddock" north of the town. This block is presumed to be the original fall and discovery site (Fig. 1).

A visit to the block (Fig. 2), about 1.6 km northwest of Bealiba, showed it to be situated on the southern slopes of a small hill. The country is now lightly wooded but was probably largely clear of trees in 1950. The block has recently been sold as part of a rural residential development.

GEOLOGY OF THE SITE

Weathered yellowish Lower Ordovician marine siltstones and shales, with a north-south strike, outcrop on the block. Some fragments of white reef quartz are also present. In such an area, a meteorite would look out of place to a keen geological observer.

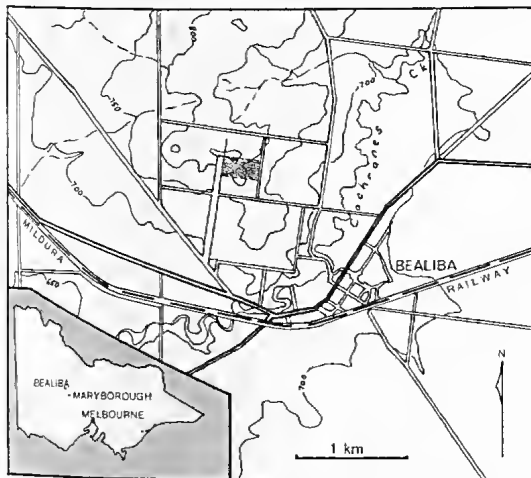


Fig. 1. Locality map showing the likely discovery and fall site of the Bealiba Meteorite, the former Renshaw paddock (stippled block), 1.6 km northwest of Bealiba, Victoria.



Fig. 2. The present-day appearance of the Renshaw paddock, in foreground, looking southeast towards Mt Bealiba.

FEATURES OF THE METEORITE

The meteorite is roughly equidimensional and measures 90 by 80 by 55 mm. Its thin, dark brown fusion crust is nearly complete, apart from where a small portion had been broken off one end, possibly on impact (Fig. 3A). The exposed area, roughly 75 by 50 mm, has the texture of weathered buff-coloured sandstone, with scat-

tered patches of dark brown iron oxide staining several millimetres across. The specimen had a mass of 652 g and a density of 3.9 g/cc prior to removal of a slice for thin sectioning. A glassy tumulose patch, 20 mm across, occurs on one surface (Fig. 3B). This feature is not associated with any internal textural variation and may have been caused by the application of a high

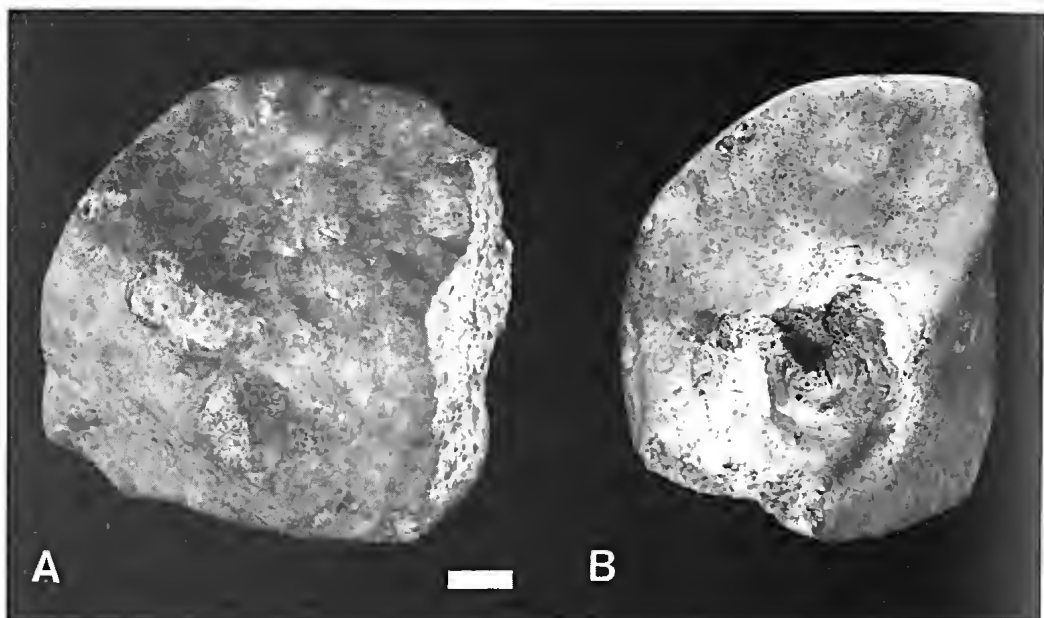


Fig. 3. The Bealiba Meteorite showing (A) fusion crust with missing portion removed on impact, and (B) tumulose patch caused by artificial heat source. Scale bar is 10 mm.

temperature heat source, such as an oxy-acetylene flame, by the finder.

PETROGRAPHY AND MINERALOGY

In thin section, the Bealiba meteorite shows plentiful but mostly poorly defined chondrules up to 2.5 mm across, together with irregular metallic grains up to 2.5 mm across, in an extensively recrystallised granular matrix which has been heavily stained with iron oxides. The main groundmass minerals are olivine, with less abundant orthopyroxene and interstitial oligoclase. Glass is absent. The chondrules may be fine-grained or barred olivine or orthopyroxene types, with minor clinopyroxene and interstitial sodian feldspar. Others consist of a distinct annulus of olivine and a core of rounded olivine grains in optical continuity (Fig. 4).

Microprobe analysis (Table 1) showed the olivine in both the groundmass and chondrules to be quite uniform in composition. Six analyses gave an average formula of $\text{Fo}_{74.6}\text{Fa}_{24.9}\text{Te}_{0.5}$ (mol%). The orthopyroxene is Mg-rich ("bron-zite") with an average composition expressed by $\text{En}_{77}\text{Fs}_{21.5}\text{Wo}_{1.5}$ (average of 5 analyses), and the uncommon clinopyroxene is diopside (Fig. 5). The interstitial oligoclase is $\text{Ab}_{83}\text{An}_{11}\text{Or}_6$.

The main metallic minerals in the meteorite are kamacite, troilite and taenite, which together



Fig. 4. Olivine chondrule 1 mm in diameter, showing distinct annular rim and etched core in optical continuity.

constitute about 5% of the stone. Kamacite occurs as irregular grains up to 2 mm across, showing as creamish white and highly reflective in incident light. Taenite is not as common and generally forms smaller grains, although some of the larger grains show the two minerals in sharp contact. The taenite may be distinguished by its slightly greyer colour, but unless the two minerals are in contact they cannot easily be distinguished optically. Troilite is as common as kamacite and forms irregular pale brownish

	1	2	3	4	5
SiO ₂	37.76	64.78	55.40	54.07	—
TiO ₂	0.02	—	0.26	0.55	3.31
Al ₂ O ₃	—	19.78	0.15	0.46	6.21
Fe ₂ O ₃	—	1.83	0.56	—	—
Cr ₂ O ₃	—	—	0.13	0.64	54.50
NiO	—	—	0.06	0.08	—
FeO	23.10	—	14.54	5.25	31.65
MnO	0.41	—	0.38	0.23	—
MgO	38.21	0.87	28.14	16.19	2.27
CaO	—	2.16	1.01	22.07	—
Na ₂ O	—	9.70	—	0.60	—
K ₂ O	—	1.12	—	—	—
Total	99.50	100.24	100.53	100.14	97.94

1. Olivine (chondrule rim) $\text{Fo}_{74.4}\text{Fa}_{25.2}\text{Te}_{0.4}$
2. Oligoclase (groundmass) $\text{Ab}_{83.4}\text{An}_{10.3}\text{Or}_{6.3}$
3. Orthopyroxene (g'mass) $\text{En}_{75.5}\text{Fs}_{22.5}\text{Wo}_{2.0}$
4. Diopside (in chondrule) $\text{En}_{46.1}\text{Wo}_{45.2}\text{Fs}_{8.7}$
5. Chromite (groundmass)

Table 1. Microprobe analyses of non-metallic minerals in the Bealiba Meteorite. Analyses obtained using Cameca and Jeol microprobes at 15 kV and specimen current 0.02 μA . Standards included corundum (Al), wollastonite (Ca, Si), pure metals (Cr, Ni, Mn), hematite (Fe), jadeite (Na), rutile (Ti) and synthetic KTa (K). Fe partitioned by stoichiometry.

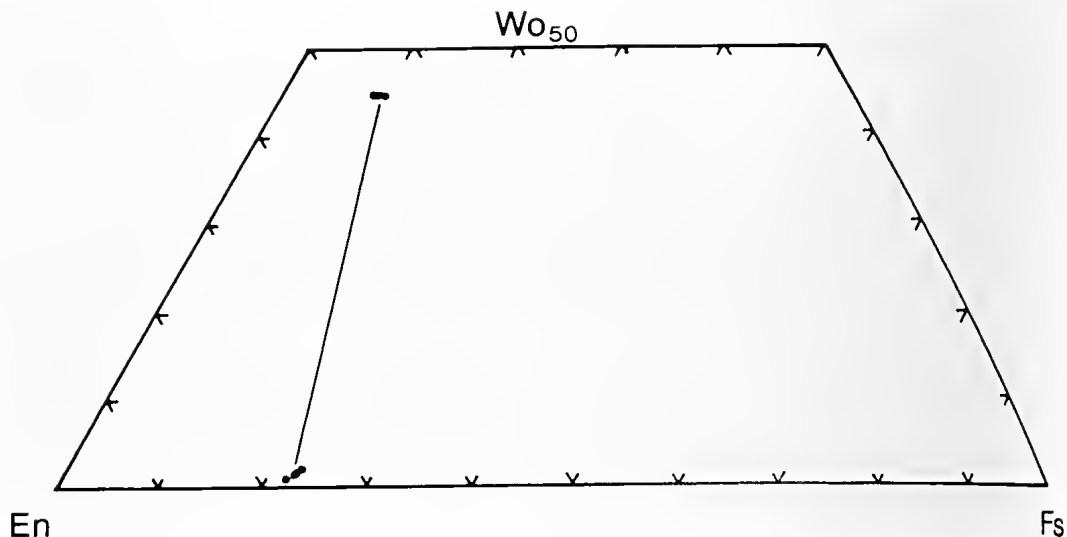


Fig. 5. Pyroxene quadrilateral showing compositions of the orthopyroxene and clinopyroxene in the Bealiba Meteorite.

pink grains up to 2.5 mm. Chromite is widespread as rounded pale grey grains up to about 0.1 mm across. Thin concretionary rims to kamacite grains consist of goethite, which also occurs as small skeletal grains and microveinlets in the groundmass. These features are a result of breakdown of the metallic minerals during weathering.

Microprobe analysis of various grains of kamacite and taenite showed compositional ranges represented by $\text{Fe/Ni} = 14\text{--}17$ and $\text{Fe/Ni} = 1.9\text{--}2.7$ (wt% basis) respectively. Cr contents were below detectable limits. The chromite contains small amounts of Al, Ti and Mg (Table 1). Chlorine-bearing areas associated with the Fe-rich alteration around kamacite grains suggest the presence of akaganéite (Buchwald & Clarke 1989).

CLASSIFICATION

A full chemical analysis of the Bealiba meteorite was not carried out but the meteorite can be classified on textural and mineralogical grounds. Summarising the criteria for chondrite classification based on Dodd (1981) and Van Schmus & Wood (1967), the Bealiba meteorite has: homogeneous olivine ($\text{Fo}_{75}\text{Fa}_{25}$) and pyroxene compositions; an orthorhombic low-Ca pyroxene; feldspar forming distinct groundmass and interstitial grains, and with composition $\text{Ab}_{83}\text{An}_{11}\text{Or}_6$; chondrules ranging from distinct to poorly defined; a matrix which is relatively

coarse-grained and recrystallised; and distinct kamacite and taenite grains. On these grounds, the Bealiba meteorite is best classified as an L6 chondrite.

CONCLUSION

Meteorite discoveries are uncommon in Victoria, although ironically the fall of the rare carbonaceous chondrite at Murchison in September 1969 is one of the best-documented and most spectacular of all known meteoritic events. Bealiba is only the tenth Victorian meteorite described (Henry 1988, Fitzgerald 1980) and the second L6 chondrite. The first L6 chondrite, the Kulnine Meteorite, is a single stone of 55 kg collected on Kulnine Station west of Mildura around 1886 (Walcott 1916). It has some unusual chemical and textural features suggestive of higher than usual crystallisation temperatures and possible "shock" recrystallisation (Mason 1973). Based on the 300 km separation of their discovery sites and their different features, the Bealiba and Kulnine meteorites represent distinct fall events.

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I am grateful for the information kindly provided by Alva and Mary Renshaw, sisters of the discoverer, the late J. E. Renshaw. Dermot Henry assisted the investigation, both in the field and in the laboratory, and Susan Henry

obtained copies of title plans for Bealiba township. Microprobe analyses were obtained in the Department of Geology, University of Melbourne, with the assistance of Pat Kelly. Brian Mason (Smithsonian Institution, Washington, DC) kindly provided information on the Kulnine meteorite.

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THE EFFECT OF THE GRAZING GASTROPOD *BEMBICIUM NANUM* ON RECOLONIZATION OF ALGAE ON AN INTERTIDAL ROCK PLATFORM

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BRALEY, H., ANDERSON, T. A. & QUINN, G. P., 1991:06:30. The effect of the grazing gastropod *Bembicium nanum* on recolonization of algae on an intertidal rock platform. *Proceedings of the Royal Society of Victoria* 103 (1): 13–16. ISSN 0035-9211.

The predominant organisms found in the littoral zone of a rock platform at Aireys Inlet, Victoria, were surveyed in autumn 1989. The predominant algal species was the brown alga *Hormosira banksii*, while the predominant invertebrate herbivore was *Bembicium nanum*. The abundances of *H. banksii* and *B. nanum* were negatively correlated. *B. nanum* had a significant effect on recolonization of the ephemeral brown alga *Scytosiphon lomentaria* but there was no effect on recolonization of *H. banksii* or of the green alga *Enteromorpha intestinalis*.

MANY RECENT studies have described the structure of intertidal communities (Cubit 1984, Lubchenco 1980, 1983, Lubchenco & Cubit 1980, Underwood 1980, 1984, Underwood & Jernakoff 1981). Many of these studies have shown that the structure of an intertidal algal community is affected by both the physical environment (including such factors as immersion) and by grazing, which may eliminate algae above a certain level on the shore (Jernakoff 1983, Steneck 1982, Underwood 1980). Whilst many experiments have examined competition between intertidal herbivores (Fletcher & Creese 1985, Fletcher & Underwood 1987, Quinn & Ryan 1989, Underwood 1984), relatively few have examined specific algal-herbivore interactions (Hunter & Hunter 1983, Underwood 1980, Underwood & Jernakoff 1981) and fewer still have been conducted in Victoria.

An initial survey of a rocky intertidal platform at Aireys Inlet, Victoria, showed a significant negative correlation between the density of the littorinid snail *Bembicium nanum* and the abundance of the predominant algal species *Hormosira banksii*. Previous studies have observed that this littorinid snail grazes micro and ephemeral algae (Quinn & Ryan 1989, Underwood 1980, 1984). A study was conducted to examine the effects of the presence of *B. nanum* upon the recolonisation of *H. banksii* and two species of ephemeral algae, *Enteromorpha intestinalis* and *Scytosiphon lomentaria*.

STUDY SITE AND METHODS

The study site was a sandstone and clay intertidal platform located at Aireys Inlet, Victoria. The platform extends from the sublittoral zone to the high water mark.

Initial Survey

An initial study was conducted to determine the abundance and total number of algae and herbivores present. Twenty one-metre square quadrats were selected randomly and the organisms within the quadrats counted. Correlation analyses were then performed between the number of plants present and the number of herbivores (Zar 1984).

Major Study

Twenty areas each measuring 200 × 200 mm were randomly selected over the rock platform. The substratum within these areas was cleaned to bare rock by scraping with a metal implement and scrubbing vigorously with a domestic scrubbing brush. The experimental areas were then bounded by a layer of antifouling paint (25% CuSO₄). Nineteen *B. nanum* (the maximum density of *B. nanum* found) were placed into each of 10 areas (inclusion) whilst all benthic herbivores were excluded from the remaining 10 areas (exclusion).

The enclosures were monitored weekly (or as close as tides and weather would permit) for

eight weeks between mid April and early June 1989. On each visit, where necessary, animals were replaced in test areas. The number of plants and algal species were recorded at each visit, and colour photographs were taken at fortnightly intervals to aid analysis of algal abundance. Variation in the mass of organic material in each experimental area was determined at the end of the experimental period. The central four centimetre square portion of each experimental area was scraped with a razor blade and the scrapings dried at 50°C for 24 hours. After weighing to the nearest 0.1 mg, the scrapings were ashed at 550°C for 24 hours and re-weighed. The loss in weight was attributed to organic matter. Analysis of variance was performed on log-transformed plant numbers and on log-transformed dry weights of organic matter found after 8 weeks in test versus control area.

RESULTS

Initial Survey

Table 1 shows the abundance of predominant organisms in the littoral zone of the rock platform. The alga *Hormosira banksii* was the predominant species, covering 100% of the substratum in the lower zones, but becoming patchy

Species	Mean	SE
<i>Hormosira banksii</i>	159.0	32.8
<i>Ulva lactuca</i>	2.8	1.2
<i>Corallina</i> spp.	1.2	0.8
<i>Siphonaria diemenensis</i>	63.9	17.2
<i>Austracochlea constricta</i>	3.7	1.4
<i>Bembicium nanum</i>	98.8	28.5

Table 1. Abundance of predominant organisms found on the rock platform (number of organisms present/m², n = 20).

and sparse in the higher zones. Small amounts of *Ulva lactuca* and *Corallina* spp. were found but no *Scytosiphon lomentaria* or *Enteromorpha intestinalis* were found in this survey. The most numerous herbivore present was *B. nanum*, averaging 98.8 animals/m² and reaching densities up to 473 animals/m² in some areas. The pulmonate limpet *Siphonaria diemenensis* was also found in large numbers. A significant negative correlation was recorded between *H. banksii* and *B. nanum* ($r = -0.705$, $df = 18$, $P < 0.001$). No other significant correlations were found.

Major Study

The ephemeral species *S. lomentaria* and *E. intestinalis* were the dominant recolonising algae

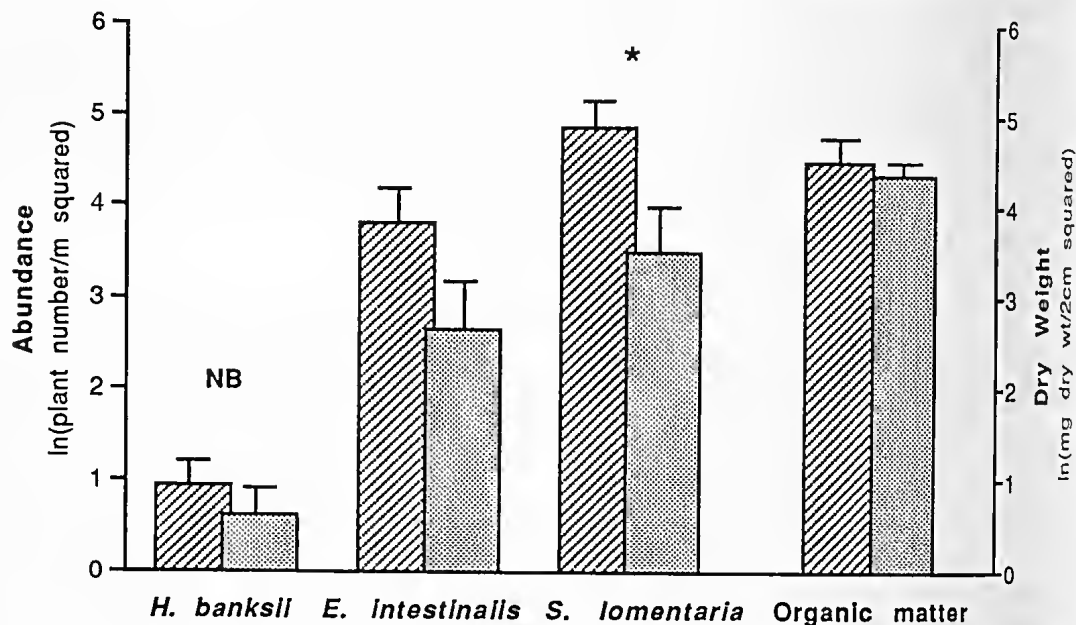


Fig. 1. Abundance of algae and dry weight of organic matter after 8 weeks following clearing of experimental areas in inclusion (diagonal rule) versus exclusion (stipple) areas. NB, analysis of *H. banksii* not performed due to the large number of null values; * = significant value of p ($p < 0.05$); inclusion = areas containing *B. nanum*; exclusion = areas where *B. nanum* excluded.

found during this experiment, covering 80–100% of the substratum in control areas and approximately 50% in test areas (those containing *B. nanum*) after 8 weeks growth (Fig. 1). Over the experimental period, *H. banksii* regrowth was greatest after 3 weeks; subsequently the number of *H. banksii* plants decreased.

The results of the analysis of variance show that *B. nanum* exhibited a significant ($F = 5.90$; $df = 1, 18$; $p = 0.026$) inhibition on the recolonisation of *S. lomentaria*. No significant effect of *B. nanum* upon *E. intestinalis* ($F = 3.15$; $df = 1, 18$; $P = 0.084$) recolonisation or upon total organic matter ($F = 0.2$; $df = 1, 18$; $P = 0.646$) was seen in this experiment. Insufficient numbers of *H. banksii* were found in the recolonisation experiment for analysis.

DISCUSSION

In this study *B. nanum* exhibited a significant negative effect on the recolonisation of *S. lomentaria* over the intertidal platform during the period mid April to early June. This phenomenon may also indirectly alter the recolonisation of other species of algae (Lubchenco 1983, Underwood 1980, Underwood and Jernakoff 1981). It has been previously noted (Quinn & Ryan 1989, Underwood 1980, 1984) that *B. nanum* grazes on ephemeral algae, such as *Ulva* spp., and on microalgae. Quinn & Ryan (1989) also observed *B. nanum* grazing upon *E. intestinalis* and *S. lomentaria* in a study conducted during winter and spring, but no evidence was given that *B. nanum* is able to restrict numbers of colonizing *S. lomentaria*.

In the present study, no direct significant effects of *B. nanum* upon *E. intestinalis* or *H. banksii* were observed. It is feasible, however, that grazers may reduce the numbers of the most competitively aggressive algal species. An initial recolonisation of the perennial *H. banksii*, which subsequently became overgrown by the opportunistic ephemeral species *S. lomentaria* and *E. intestinalis*, suggests that grazing gastropods such as *B. nanum* may enhance the recolonisation of *H. banksii* over a longer period. Despite the reduction in the number of *S. lomentaria* in areas where *B. nanum* was present, no significant reduction of total organic matter was observed. Since the organic matter was measured in the central region of each experimental area, this latter result may reflect the patchy nature of the recolonisation of the algae rather than an effect of grazing. A longer study may clarify these points.

Experimental areas were bounded by a layer of antifouling paint (adjusted to 25% CuSO_4). The toxic effects of copper are believed to repel gastropods and prevent them from crossing a barrier of such paint (Cubit 1984). Antifouling paint was used in preference to cages in order to alleviate cage effects such as a reduction in wave and wind action, shading and harbouring of water and food particles (Cubit 1984, Underwood 1980). These microclimatic changes may also be compounded by the growth of algae on cages and by the presence of roofs on cages (Underwood 1980). Antifouling paint did not prevent *B. nanum* leaving the enclosures, and missing animals were replaced when necessary, although no *B. nanum* entered the control areas. Loss of animals from test areas was greater in the lower zones and may have been due to increased wave action and immersion in these zones.

In conclusion, *B. nanum* has been seen to exert a significant effect over the recolonisation of the ephemeral brown alga *Scytosiphon lomentaria* in the late autumn to early winter period in Victoria. *B. nanum* thus plays a recognizable role in the structure of this intertidal community.

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**GALAXIAS BREVIPINNIS GÜNTHER (PISCES, GALAXIIDAE)
IN NORTH-EASTERN VICTORIA: FIRST RECORDS FOR
THE MURRAY-DARLING DRAINAGE BASIN**

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MORISON, A. K. & ANDERSON, J. R., 1991:06:30. *GALAXIAS BREVIPINNIS* Günther (Pisces, Galaxiidae) in north-eastern Victoria: first records for the Murray-Darling drainage basin. *Proceedings of the Royal Society of Victoria* 103 (1): 17-28. ISSN 0035-9211.

During surveys in 1990, *Galaxias brevipinnis* Günther, 1866 was caught at 11 sites in two catchments in north-eastern Victoria, the first reports of this species from the Murray-Darling drainage basin. Data on gonad maturity stage, gonadosomatic index and maximum oocyte diameter indicate that the species has established breeding populations that spawn in April or early May. Assessment of past survey results indicates that these populations are most probably recently introduced rather than being undiscovered natural populations. Movement of *G. brevipinnis* from the upper Snowy River catchment through tunnels carrying water for hydro-electric and irrigation purposes is regarded as the most likely means of introduction but other possibilities are discussed. Specimens were collected from several types of stream habitat including rocky fast-flowing habitats and one site with fine sediments and slow flow. Occurrence of the species was independent of the presence of *Salmo trutta* L. The spread of *Galaxias brevipinnis* may adversely affect other aquatic species indigenous to the Murray-Darling drainage basin.

THE FAMILY Galaxiidae contains about 40 species of small salmoniform fishes of the Southern Hemisphere including 22 species from southern Australia (Allen 1989). Galaxiids constitute a major proportion of the total number of freshwater fish species native to southern Australia (McDowall & Frankenberg 1981). However, only three species of galaxiids are included among the list of about 31 species of native freshwater fish found in the Murray-Darling Basin, the largest drainage basin in Australia. Those three species are the mountain galaxias, *Galaxias olidus* Günther, 1866, the flat-headed galaxias, *G. rostratus* Klunzinger, 1872, and the diadromous common galaxias, *G. maculatus* (Jenyns, 1842) (Anderson 1989, Pierce 1989).

In Australia, *G. brevipinnis* Günther, 1866 is found in coastal drainages from Sydney to Adelaide, and in Tasmania; it is also found in New Zealand, the Chatham Islands, and the Auckland and Campbell Islands (McDowall 1980b). It is a relatively large, elongate fish known to reach 278 mm, with thick, fleshy fins and usually with a distinct blue-black patch above the base of the pectoral fin (McDowall 1980b). It is usually found in small, clear-flowing, forested streams, where it often inhabits rocky areas with fast-flowing water, and in lakes where it is reported as either living among rocks on the lake bed or evenly distributed throughout the body of

water (Andrews 1976, McDowall 1980b). *G. brevipinnis* is an amphidromous species having a marine "whitebait" juvenile stage in New Zealand, Tasmania and on the Australian mainland, although this is believed to be a facultative rather than obligatory phase to its life-cycle (McDowall & Frankenberg 1981). Spawning is believed to take place in streams in autumn or early winter (Koehn & O'Connor 1990); newly-hatched young go to sea for several months and return when 45-50 mm long (McDowall 1980b). However, many land-locked populations have been reported from lakes in New Zealand and Tasmania, and from one lake on the Australian mainland (McDowall & Frankenberg 1981).

G. brevipinnis has not been recorded previously from the Murray-Darling system (Allen 1989), although it is present in coastal streams on the Fleurieu Peninsula in South Australia near the mouth of the River Murray (McDowall & Frankenberg 1981). In this paper we document the first records of *G. brevipinnis* from the Murray-Darling Basin and discuss the possible reasons for the species' newly discovered presence.

METHODS

Map grid references, stream names, altitudes (from the 1:100,000 National Topographic Map

Series) and dates of sampling at the 50 sites sampled (Figs 1 and 2) are given in the Appendix.

On 26 January 1989 and 21 March 1990 single-wing fyke nets (mesh size 25 mm and funnel opening 200 mm) were used in Koetong Creek (site 31). During the more intensive survey between 23 March and 1 June 1990 a shore-mounted, pulsed DC electrofisher (H. Riddle 1KWC model) powered by a Honda portable generator (model EG 1900X, maximum output 1.9 KVA) was used. At most sites, a stream section about 100 m long was sampled; shorter sections were sampled when access was limited or a large number of fish were caught. We maximised our chances of finding populations of *G. brevipinnis* by sampling small streams with rocky substrates, often in the headwaters of catchments, although ease of access also determined eventual sampling sites.

Descriptions given by McDowall (1980a), Cadwallader & Backhouse (1983) and Merrick & Schmida (1984) were used to identify specimens, but all *Galaxias* specimens and a representative sample of other native species were preserved for confirmation of identity. Specimens were fixed in 10% neutralised formalin for a minimum of 3 days and then transferred for one day to 40% ethanol, then to 60% ethanol, and finally they were preserved in 70% ethanol. The standard length of each preserved *G. brevipinnis* specimen was measured to the nearest 1 mm with dial callipers, and weights of whole fish and their gonads were measured to the nearest 0.01 g on a Mettler PE3600 digital balance. The gonads of each *G. brevipinnis* specimen were examined macroscopically and their maturity stage was estimated according to the scheme used by Humphries (1989): Stage I, virgin; Stage II, recovering spent; Stage III, developing; Stage IV, mature; Stage V, ripe; Stage VI, spent. As a further indication of the stage of gonad development, the gonadosomatic index (GSI) was calculated as weight of gonad/total weight of fish \times 100. Maximum oocyte diameters were measured with an eyepiece micrometer on a Zeiss

stereomicroscope at $40\times$ magnification. Data on size and reproductive condition of female *G. brevipinnis* collected at sites surveyed during 21–30 March were combined, as were data on females collected during May 1990. Data on size and reproductive condition of males collected during 23–29 March 1990 were combined, as were those for males collected during 28 May–1 June 1990.

The number of vertebrae, excluding hypural centra, of *G. brevipinnis* from north-eastern Victoria were counted on x-ray negatives taken of the preserved specimens in the Ichthyology Department, Museum of Victoria. The significance of differences in these vertebral counts among populations of *G. brevipinnis* was tested using a single factor analysis of variance followed by a Newman-Keuls multiple range test (Zar 1974). Data for other populations of *G. brevipinnis* in Australia were obtained from McDowall & Frankenberg (1981, Table 1). Only populations with data from 10 or more specimens were used in the analysis.

To test whether the frequencies of occurrence of *G. brevipinnis*, *G. olidus* and *S. trutta* were independent of each other, we tested 2×2 contingency tables by using the chi-square test with the Yates correction for continuity (Zar 1974).

Information on the known distribution of *G. brevipinnis*, records of other species of *Galaxias* from the survey area, and locations surveyed in the past were obtained from Tunbridge (1978), McDowall & Frankenberg (1981), Cadwallader & Backhouse (1983), Brumley et al. (1987), and Koehn & O'Connor (1990). In addition, the collections of the Australian Museum, Sydney, and the Museum of Victoria, Melbourne, were checked for all records of *Galaxias* species in the upper Murray, Kiewa, upper Murrumbidgee and upper Snowy River catchments. Unpublished records from surveys by the Victorian Fisheries Division (Baxter 1985, 1988, 1989, 1990 and pers. comm., and Cadwallader pers. comm.) were also checked.

All preserved specimens of *G. brevipinnis* and

Date	Sex	Standard Length (mm)		Maturity Stage (n)				GSI (%)		Max. Oocyte Diameter (mm)	
		mean	range	II	III	IV	Total	mean	range	mean	range
21–30 March	Females	98	78–137	2	0	10	12	11.6	0.28–18.8	1.10	0.08–1.40
28–31 May	Females	124	85–150	2	3	0	5	0.61	0.36–0.99	0.37	0.16–0.76
23–29 March	Males	89	75–114	0	1	6	7	11.4	4.32–17.3		
28 May–1 June	Males	86	67–113	3	1	2	6	3.59	0.14–11.8		

Table 1. Size and reproductive condition of female and male *G. brevipinnis* collected between 21 March and 1 June 1990.

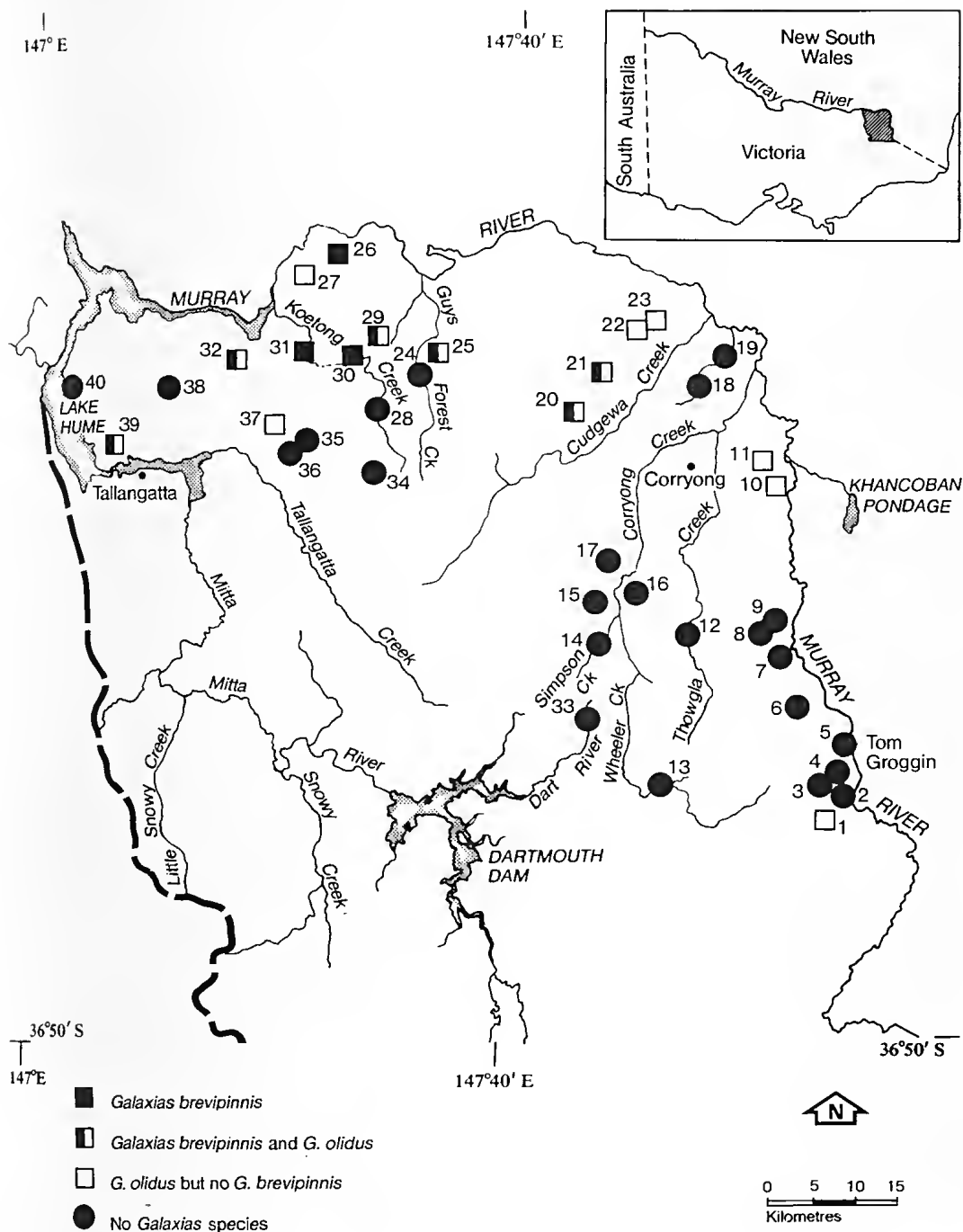


Fig. 1. Sampling sites in north-eastern Victoria upstream of Hume Dam showing locations where *Galaxias brevipinnis* and *G. olidus* were caught (January 1989–June 1990). Details of site locations and other fish species caught are given in the appendix.

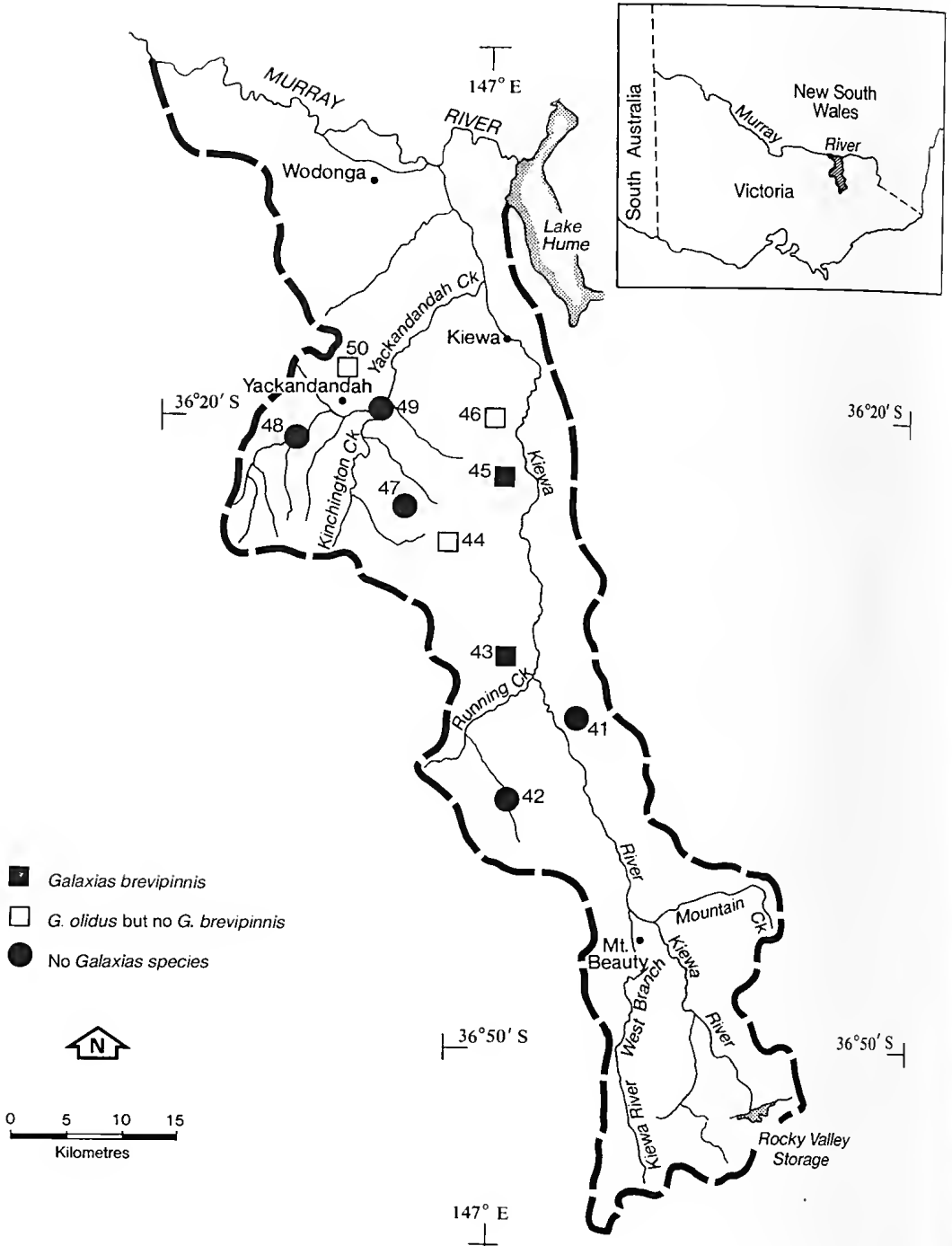


Fig. 2. Sampling sites in the Kiewa River catchment showing locations where *Galaxias brevipinnis* and *G. olidus* were caught (May–June 1990). Details of site locations and other fish species caught are given in the appendix.

G. olidus have been lodged at the Museum of Victoria.

RESULTS

The numbers of each fish species caught at each of the 50 sites sampled between 21 March and 1 June 1990 are given in the Appendix. *G. brevipinnis* was caught at 11 sites, nine of which were in the catchment of the upper River Murray and two in the catchment of the Kiewa River (Figs 1 and 2).

Distribution of *G. brevipinnis*

On 26 January 1989 three specimens of *G. brevipinnis* were collected from one rocky pool in Keotong Creek (site 31). The only other species of fish collected from this site were the exotic brown trout, *Salmo trutta*, and rainbow trout, *Oncorhynchus mykiss*, although the two-spined blackfish, *Gadopsis bispinosus*, was recorded 2 km downstream below a series of falls. On 21 March 1990 another specimen of *G. brevipinnis* was collected at site 31 and three more specimens from further upstream (site 30). Between 23 March 1990 and 1 June 1990 *G. brevipinnis* were recorded at nine sites extending from Jarvis Creek near Tallangatta (site 39) upstream to an unnamed tributary of Cudgewa Creek, 13 km north-west of Corryong (site 20, Fig. 1). Five of these sites were in small streams draining directly into Lake Hume and four sites were in small streams draining directly into the River Murray or its tributaries.

Because these results indicated that *G. brevipinnis* was widely distributed in the catchment of the Hume Weir, sampling was extended to the catchment of the Kiewa River, the first major tributary entering the River Murray below the weir. *G. brevipinnis* was recorded from two of the ten sites sampled on tributaries of the lower reaches of the Kiewa River (Fig. 2).

G. brevipinnis was caught at sites within an altitude range of 210–530 m; the range for all sites was 210–790 m. At sites where *G. brevipinnis* was caught streams ranged from the very small (widths less than 1 m; maximum depths about 300 mm (sites 20, 43)) to larger (widths 5 m; maximum depths of pools more than 2 m (site 31)). These sites, like most sites we selected, frequently had rock and boulder substrates, but *G. brevipinnis* was also recorded at one site (site 45) where the substrate was predominantly sand and finer sediment and where the stream flowed comparatively slowly.

Riparian vegetation at the sites where *G. brevipinnis* was caught ranged from essentially undisturbed native vegetation (sites 29–31, 43) to introduced grasses on grazing land (site 39) or introduced trees (site 45). *G. brevipinnis* was also caught in pools in the headwater sections of intermittent streams which became subterranean further downstream (sites 26, 39).

Co-habiting species

G. olidus was found at 16 sites, including six sites (sites 20, 21, 25, 29, 32 and 39) where *G. brevipinnis* was also caught. A chi-square test of the 2 × 2 contingency table indicated that the presence of *G. brevipinnis* was independent of the presence of *G. olidus* ($X^2 = 2.079$, $p > 0.05$).

Salmo trutta was found with *G. brevipinnis* at five sites (Sites 30, 31, 39, 43, and 45), with *G. olidus* at four sites (Sites 1, 10, 37, 39) and alone at 23 other sites. Chi-square tests indicated that the presence of *S. trutta* had a significant effect on the presence of *G. olidus* ($X^2 = 8.621$, $P < 0.01$) but that the presence of *G. brevipinnis* was independent of the presence of *S. trutta* ($X^2 = 0.862$, $P > 0.05$).

The only other species of fish found with *G. brevipinnis* were *Gadopsis bispinosus* (site 21) and *Oncorhynchus mykiss* (sites 30, 31, and 43). Other species recorded during the surveys were freshwater blackfish, *Gadopsis marmoratus* (sites 4, 12 and 38), southern pigmy-perch, *Nannoperca australis* (site 46) and redfin, *Perca fluviatilis* (site 37).

Reproductive condition

Comparisons of the maturity stages, GSI and maximum egg diameters for *G. brevipinnis* collected in March, May and June indicate that spawning had taken place in April or early May. In samples collected later the proportion of fish with more mature gonads (Stage IV) was smaller, mean GSI values for both females and males were much lower, and the maximum size of oocytes was also much smaller. These differences are not due to differences in the size of fish caught in the two time periods: the later samples contained more larger female fish, and the mean size and the size range of males were similar (Fig. 3, Table 1). Between these sampling periods water temperatures were falling and stream flows had substantially increased following rainfall over the area in mid-April. After further heavy rainfall, sampling on 17–18 May was curtailed because high water velocities and high

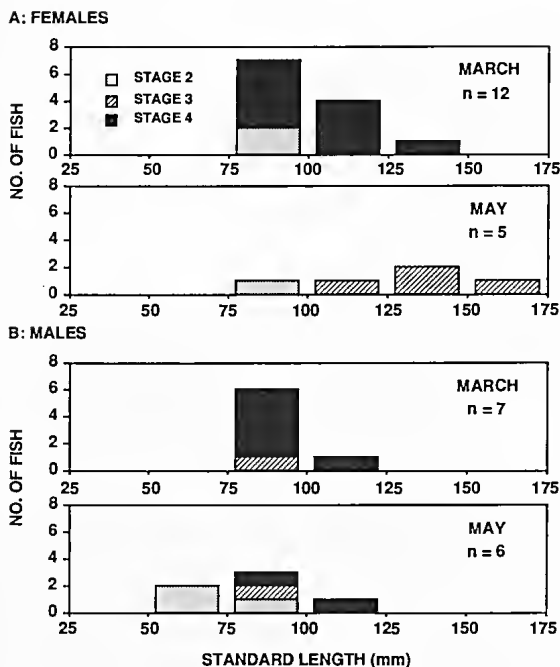


Fig. 3. Length-frequency histograms showing maturity stage for (A) female and (B) male *Galaxias brevipinnis* caught in March and May 1990.

turbidity made efficient electrofishing impossible.

Vertebral morphology

An analysis of variance of the mean number of vertebrae of *G. brevipinnis* in our samples and in 10 of those studied by McDowall & Frankenberg (1981) showed significant differences among the samples ($F = 17.85$, $P < 0.001$). However, a Newman-Keuls test could not separate samples into distinct groups.

DISCUSSION

Our survey results indicate that populations of *G. brevipinnis* are present at 11 sites in nine streams in catchments in north-eastern Victoria. Moreover the distribution of the 11 sites, the size range of *G. brevipinnis* we caught and their reproductive condition suggest that the species has been present for several years at least and has established breeding populations that spawn in April or early May. The populations reported here may be part of the natural range of the species, and perhaps remnants of a once wider distribution within the Murray-Darling Basin,

or they may be recently established populations.

Pre-1989 surveys

Fish surveys carried out prior to 1989 at 89 sites in the Upper Murray catchment and 29 sites in the Kiewa River catchment recorded no specimens of *G. brevipinnis*, suggesting that the species has recently extended its range into the Murray-Darling drainage basin. These surveys included multiple samples from all major tributaries and were widely distributed between their headwater and lowland sections. Sampling methods included dip-netting (27 sites), electrofishing (4 sites), fyke nets (5 sites), and the use of the piscicide rotenone (77 sites). The surveys recorded *Galaxias* spp. at 35 sites, including both *G. olidus* (32 sites) and *G. rostratus* (3 sites near Albury). We expect that *G. brevipinnis*, if present in the area, would also have been caught even though none of the pre-1989 sampling sites coincided exactly with sites where we caught *G. brevipinnis*.

It is possible that *G. brevipinnis* was caught during these earlier surveys but was not correctly identified. However, all the specimens in the Museum of Victoria have been recently examined by T. Raadik (formerly of the Museum's Department of Ichthyology) who found no *G. brevipinnis* among the many collections of *G. olidus* from north-eastern Victoria. Specimens of *G. olidus* reported from north-eastern Victoria by McDowall & Frankenberg (1981) were carefully examined by those authors and they reported no *G. brevipinnis*. Species of *Galaxias* recorded during Fisheries Division surveys have not always been unambiguously identified but no specimens of *G. brevipinnis* have been collected. Small specimens of *Galaxias* can be difficult to identify in the field but, because *G. brevipinnis* grows much larger than *G. olidus* and *G. rostratus* (the only other galaxiids known to inhabit the same area), the larger specimens are readily distinguishable. Presumably *G. brevipinnis* would have been correctly identified among the larger specimens.

Murray-Darling populations

The April-May spawning period indicated for *G. brevipinnis* in north-eastern Victoria is within the autumn or early winter spawning period previously reported for *G. brevipinnis* in mainland Australia (Frankenberg 1969, Koehn & O'Connor 1990), Tasmania (Andrews 1976) and New

Zealand (McDowall 1970). However, land-locked (and usually lacustrine) populations of normally diadromous galaxiids frequently exhibit shifts in spawning period and migration patterns compared with riverine populations and migrate upstream in spring to spawn in streams (Pollard 1971, Andrews 1982, Humphries 1989). Populations of *G. brevipinnis* in north-eastern Victoria are effectively land-locked because of their distance from the sea (2,225 km from Lake Hume to the mouth of the River Murray) and because of the barriers impeding a return migration of juvenile fish. It is not known whether larvae of *G. brevipinnis* in north-eastern Victoria move downstream after hatching as do those in coastal streams, but such a movement would lead them eventually to Lake Hume (or Lake Mulwala for Kiewa River populations). Consequently, recruitment probably depends on juveniles which remain upstream of Lake Hume. Regular recruitment from the Snowy catchment or from the Murray seems unlikely. *G. brevipinnis* has not yet been found in Lake Hume and details of any migratory movements of these populations are unknown.

Origin of parent stock

G. brevipinnis from South Australian populations near the mouth of the River Murray may have moved upstream into north-eastern Victoria, but such a movement would have involved an upstream migration of more than 2,000 km, past two large dams (Yarrawonga Weir and Hume Dam) and 13 smaller weirs. It seems improbable that such a migration would be successful in recent times but not during the thousands of years prior to European settlement. Moreover, if such a movement had occurred we would expect that *G. brevipinnis* would have been found in other tributaries entering the River Murray further downstream.

It is more plausible that *G. brevipinnis* was deliberately or inadvertently released into the catchment of the upper River Murray. We do not regard *G. brevipinnis* as a natural part of the fish fauna of north-eastern Victoria. There are several potential sources and modes of introduction for the *G. brevipinnis* now found in this area (and these origins are not mutually exclusive).

Consignments of trout from hatcheries within the natural range of *G. brevipinnis* have been released into streams in the upper Murray, and these consignments may have included some specimens of *G. brevipinnis*. The species may have been illegally stocked into streams, other

public waters or private waters from which escape occurred. Specimens of *G. brevipinnis* may also have been transported inland for aquarium specimens or as live bait and escaped into the wild. Evidence for any of these events is lacking.

The most likely route by which *G. brevipinnis* gained access to north-eastern Victorian waters is via the Snowy Mountains Scheme by which water is diverted from the upper Snowy River catchment to the upper River Murray for irrigation and the generation of hydro-electricity (Fig. 4). *G. brevipinnis* has been recorded at sites in the upper Snowy River catchment, including the Snowy River below Eucumbene Dam (McDowall & Frankenberg 1981; collected 1973, J. Paxton pers. comm.), and four creeks draining to Lake Eucumbene (Tilzey 1976, as *G. coxii* = *G. brevipinnis*).

Snowy Mountains Scheme

The volume of water diverted annually by the Snowy Mountains Scheme is about 580 GL, but this volume may almost double in dry years and comprise about one-third of the total inflow to Lake Hume (Jacobs 1989). Some of the water flows by gravity from the Island Bend Pondage on the upper Snowy River to the Geehi Reservoir in the River Murray catchment through the 14.4 km-long Snowy-Geehi tunnel (Fig. 4). Additional water flows by gravity from Lake Eucumbene to the same tunnel via the 23.5 km-long Eucumbene-Snowy Tunnel, or is pumped from Lake Jindabyne via the 9.9 km long Jindabyne-Island Bend Tunnel (Snowy Mountains Hydro-electric Authority 1982). Fish would have little difficulty moving through these tunnels: screens on tunnel entrances are large relative to fish size, and the tunnel gradients are generally small (flow can be in either direction in some tunnels depending on levels in the storages).

The rock wall of Geehi Dam (slope 2:1 and vertical height difference between full supply level and dam crest of 5.49 m) would not be a significant barrier to *G. brevipinnis* gaining access to the river downstream. The species is noteworthy for its ability to climb steep waterfalls and moist rocky faces by using its pectoral and pelvic fins, and to move great distances inland past formidable barriers (McDowall & Frankenberg 1981).

Another route by which *G. brevipinnis* or other species of fish could move into the Murray-Darling drainage basin is via the Eucumbene-

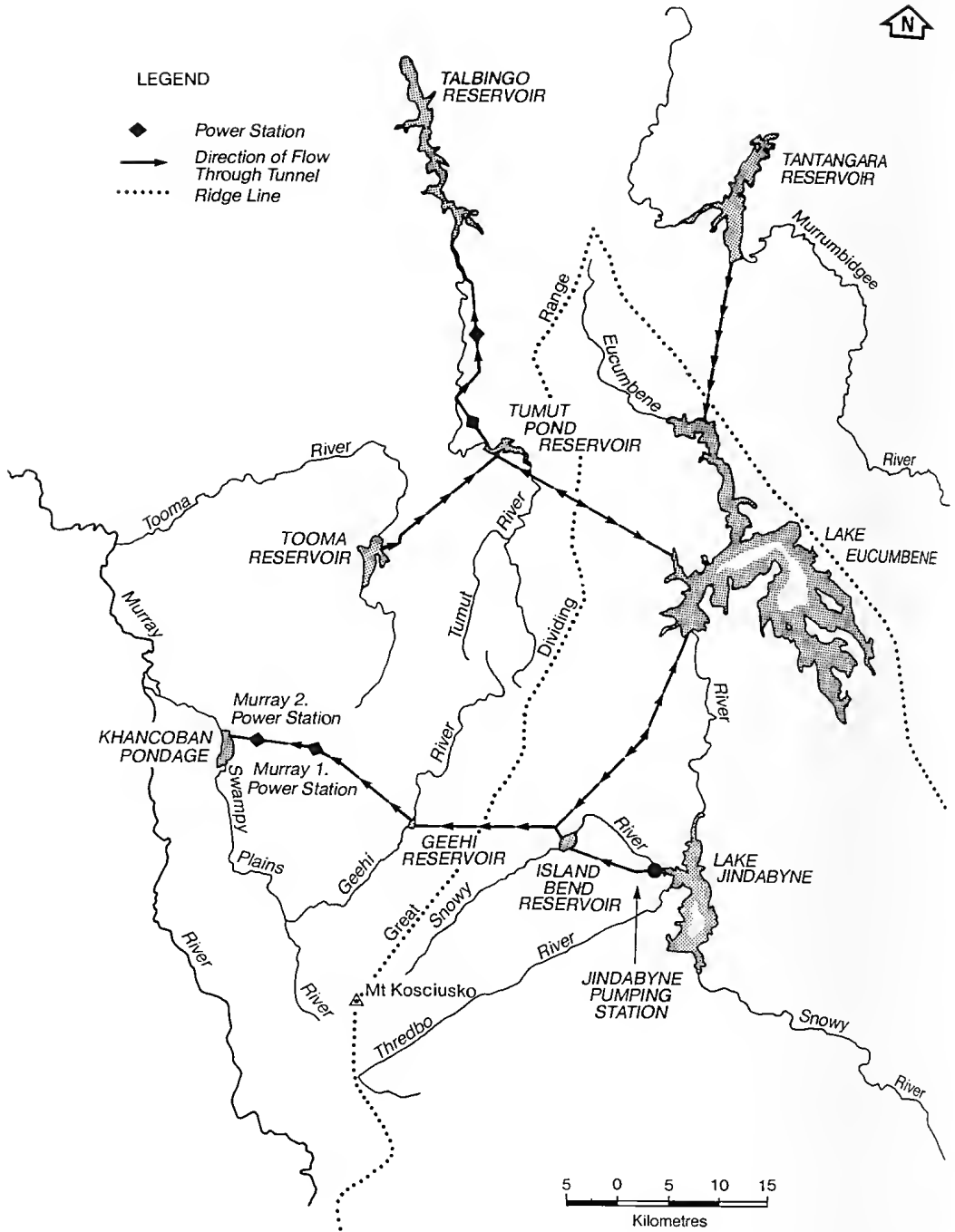


Fig. 4. Map of the Snowy Mountains area showing routes for diversions of water between catchments.

Tumut Pond Tunnel (Fig. 4). Conversely, the Tantangara-Eucumbene connection could provide fish access from the Murray-Darling catchment to the Snowy River catchment.

Vertebral morphology

Evidence for the source of the parent stock of *G. brevipinnis* populations may be obtained from the vertebral morphology of specimens. McDowall & Frankenberg (1981) reported a trend among populations of *G. brevipinnis* for an increasing number of vertebrae with increasing latitude. The frequency distribution of the number of vertebrae in *G. brevipinnis* from north-eastern Victoria (Fig. 5) has a higher mode than

that of other populations in Victoria, South Australia or New South Wales and most closely resembles those of more southerly populations in Tasmania and New Zealand. Although the differences are not significant and there is a need for more specimens to be analysed, the data suggest that the north-eastern Victorian population may be unlike those in South Australia and New South Wales. The distribution may be characteristic of the parental stock but may have been influenced by environmental factors during development, by the random effects of a population bottleneck during the early colonisation phase, or by sampling bias. No other morphological characteristics of *G. brevipinnis* allow different populations to be differentiated (McDowall & Frankenberg 1981).

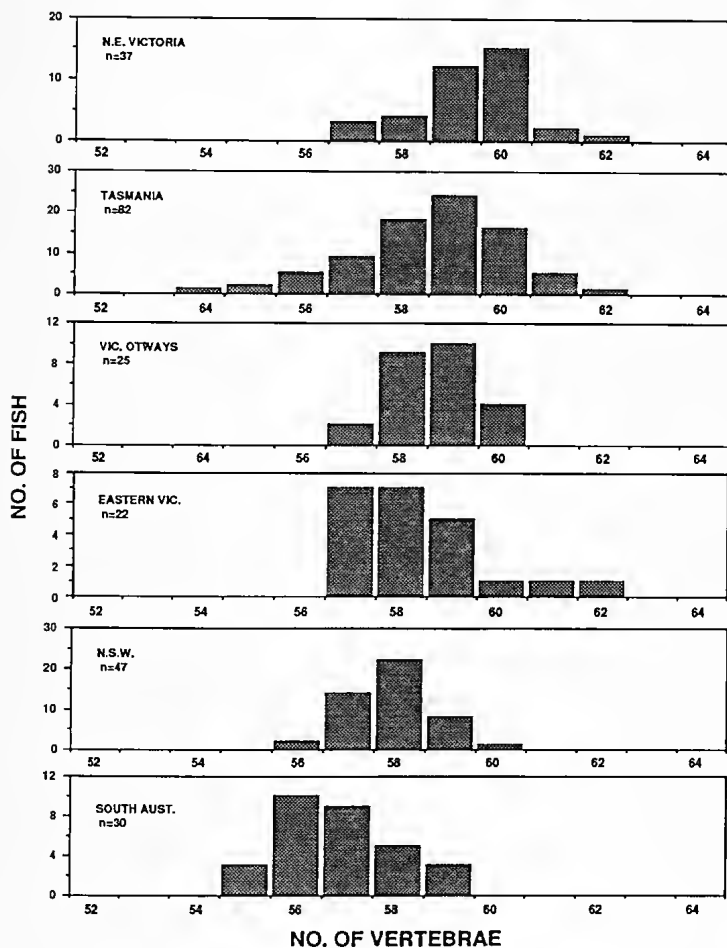


Fig. 5. Frequency distributions of number of vertebrae in *Galaxias brevipinnis* from north-eastern Victoria and from localities listed in McDowall & Frankenberg (1981).

Further work

Biochemical methods of examining variation among populations of *G. brevipinnis*, such as electrophoresis and mitochondrial DNA analysis, may provide more conclusive evidence as to the source of populations in north-eastern Victoria and therefore indicate the likely mechanism of their introduction.

The introduction of *G. brevipinnis* to streams in north-eastern Victoria may lead to increased competition with indigenous species, in particular *G. olidus*. *G. brevipinnis* and *G. olidus* normally do not occur together in coastal streams (McDowall & Frankenberg 1981), although recent surveys in the Otways region recorded *G. brevipinnis* at two of the three sites at which *G. olidus* occurred (Koehn & O'Connor 1990). There has been some concern that *G. brevipinnis* has expanded its range in Tasmania at the expense of other galaxiid species (W. Fulton, Inland Fisheries Commission, Tasmania, pers. comm). Other species of fish such as *Gadopsis bispinosus*, which are not naturally sympatric with *G. brevipinnis*, may also be adversely affected by this addition to the local fish fauna.

Further work will be needed to clarify the source, status and reproductive cycle of populations of *G. brevipinnis* in north-eastern Victoria. Further survey work may record additional populations in the Murray-Darling Basin, would allow any potential expansion of known populations and the response of indigenous species to be monitored, and could also identify key features of the life cycle of this normally amphidromous species.

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APPENDIX

Date of survey, location, altitude and numbers of each fish species caught at each sample site. Basin 01E is the River Murray catchment upstream of the Mitta Mitta River, Basin 01W is the Mitta Mitta catchment, and Basin 02 is the Kiewa River catchment. P = species recorded at site on preliminary survey on 28 March 1990; Trib. = unnamed tributary.

SITE NO.	DATE	LOCATION	BASIN NO.	MAP NO.	GRID REF.	ALTI-TUDE	C A T C H							
							<i>Galaxias brevipinnis</i>	<i>G. olidus</i>	<i>Gadopsis marmoratus</i>	<i>G. bispinosus</i>	<i>Nannoperca australis</i>	<i>Salmo trutta</i>	<i>Oncorhynchus mykiss</i>	<i>Perca fluviatilis</i>
1	16.5.90	Buckwong Ck.	01E	8524	009520	550	-	1	-	-	-	2	-	-
2	16.5.90	Murray R. Trib	01E	8524	005544	570	-	-	-	-	-	-	-	-
3	16.5.90	Boggy Ck.	01E	8524	977550	600	-	-	-	-	-	4	-	-
4	16.5.90	Ormeo Ck.	01E	8524	993571	540	-	-	-	-	-	3	1	-
5	16.5.90	Stony Ck.	01E	8525	002613	600	-	-	-	-	-	5	1	-
6	15.5.90	Surveyors Ck.	01E	8525	943663	550	-	-	-	-	-	12	12	-
7	15.5.90	Lt. Bunroy Ck.	01E	8525	926723	380	-	-	-	-	-	12	-	-
8	15.5.90	Ironpot Ck.	01E	8525	902736	520	-	-	-	-	-	9	-	-
9	15.5.90	Bunroy Ck.	01E	8525	907752	500	-	-	-	-	-	12	-	-
10	15.5.90	Biggara Ck.	01E	8525	905847	340	-	1	-	1	-	8	-	-
11	15.5.90	Murray R. Trib.	01E	8525	905905	360	-	24	-	-	-	-	-	-
12	18.5.90	Thowgla Ck.	01E	8425	827766	440	-	-	3	-	-	4	4	-
13	17.5.90	Cattlemans Ck.	01E	8424	786553	790	-	-	-	-	-	9	2	-
14	17.5.90	Simpson Ck.	01E	8425	703717	510	-	-	1	-	-	12	7	-
15	30.5.90	Boyd Ck.	01E	8425	698767	460	-	-	-	1	-	4	34	-
16	18.5.90	Star & Jones Ck.	01E	8425	745796	400	-	-	-	-	-	2	-	-
17	30.5.90	Rawes Ck.	01E	8425	730845	300	-	-	-	-	-	16	3	-
18	18.5.90	Horse Ck.	01E	8425	818037	500	-	-	-	-	-	-	-	-
19	18.5.90	Horse Ck.	01E	8425	850060	260	-	-	-	-	-	-	-	-
20	28.5.90	Cudgewa Ck Trib.	01E	8425	685995	420	4	25	-	-	-	-	-	-
21	28.5.90	Stony Ck.	01E	8425	690061	430	2	6	-	6	-	-	-	-
22	30.5.90	Pine Mountain Ck	01E	8425	753097	440	-	69	-	-	-	-	-	-
23	30.5.90	Pine Mountain Ck	01E	8425	766113	340	-	106	-	-	-	-	-	-
24	29.3.90	Burrowye Ck.	01E	8425	487047	400	-	-	-	-	-	5	-	-
25	29.3.90	Jones Ck.	01E	8425	496072	320	12	3	-	-	-	-	-	-
26	30.3.90	Flaggy Creek	01E	8325	404156	410	1	-	-	-	-	-	-	-
27	29.5.90	Stockyard Ck	01E	8326	354167	290	-	26	-	-	-	-	-	-
28	28.3.90	Koetong Ck.	01E	8325	440985	580	-	-	-	-	-	18	-	-
29	29.5.90	Jimney Ck.	01E	8325	432065	530	2	69	-	-	-	-	-	-

SITE NO. DATE	LOCATION	BASIN NO.	MAP NO.	GRID REF.	ALTI- TUDE	C A T C H							<i>Salmo trutta</i>	<i>Oncorhynchus mykiss</i>	<i>Perca fluviatilis</i>
						<i>Galaxias brevipinnis</i>	<i>G. olidus</i>	<i>Gadopsis marmoratus</i>	<i>G. bispinosus</i>	<i>Nannoperca australis</i>					
30 23.3.90	Koelong Ck.	01E	8325	401049	470	3	-	-	-	-	-	1	15	-	-
31 21.3.90	Koelong Ck.	01E	8325	352064	280	1	-	-	-	-	-	2	2	-	-
32 27.3.90	Cottonree Ck.	01E	8325	276035	240	5	29	-	-	-	-	-	-	-	-
33 17.5.90	Dart R.	01W	8425	697625	740	-	-	-	-	-	-	5	1	-	-
34 28.3.90	Dry Forest Ck.	01W	8325	424907	720	-	-	-	-	-	-	-	-	-	-
35 29.5.90	Dry Forest Ck.	01W	8325	372958	320	-	-	-	-	-	-	5	-	-	-
36 28.3.90	Dry Forest Ck.	01W	8325	358953	290	-	-	-	6	-	-	2	7	-	-
37 29.5.90	Kangaroo Ck.	01W	8325	313974	240	-	5	-	P	-	-	2	P	5	-
38 27.3.90	George's Ck.	01W	8325	220012	320	-	-	13	-	-	-	-	-	-	-
39 27.3.90	Jarvis Ck.	01W	8325	147944	210	1	2	-	-	-	-	1	-	-	-
40 27.3.90	Bethanga Ck.	01W	8325	067006	190	-	-	-	-	-	-	-	-	-	-
41 01.6.90	Bay Ck.	02	8324	105507	340	-	-	-	-	-	-	17	-	-	-
42 01.6.90	Running Ck.	02	8324	014460	380	-	-	-	-	-	-	21	10	-	-
43 01.6.90	House Ck.	02	8324	006566	380	1	-	-	-	-	-	1	5	-	-
44 31.5.90	Glen Ck.	02	8325	947665	400	-	-	-	-	-	-	26	-	-	-
45 31.5.90	Hellhole Ck.	02	8225	005744	260	3	-	-	-	-	-	2	-	-	-
46 01.6.90	Gap Ck.	02	8325	009799	220	-	7	-	-	1	-	-	-	-	-
47 31.5.90	Kinchington Ck Trib.	02	8225	924751	360	-	135	-	-	-	-	-	-	-	-
48 31.5.90	Nine Mile Ck Trib.	02	8225	821773	360	-	-	-	-	-	-	10	1	-	-
49 31.5.90	Yackandandah Ck.	02	8225	912817	250	-	-	-	-	-	-	3	-	-	-
50 31.5.90	Basin Ck.	02	8225	870840	300	-	76	-	-	-	-	-	-	-	-

AUSTRALASIAN TERTIARY BRACHIOPODA. THE SUBFAMILY ANAKINETICINAE NOV.

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RICHARDSON, J. R. 1991:06:30. Australasian Tertiary Brachiopoda. The subfamily Anakineticinae. *Proceedings of the Royal Society of Victoria* 103 (1): 29–45. ISSN 0035-9211.

Four new endemic brachiopod genera (*Adnatida*, *Aliquantula*, *Elderra*, *Pilkena*) and seven new species (*Anakinetica breva*, *A. recta*, *A. tumida*, *Magadinella hamiltonensis*, *Pilkena compressa*, *Adnatida gngangarensis* and *Elderra toorloensis*) are described from Tertiary bryozoan sands in Victoria, South Australia and Western Australia. The taxa are included in the new subfamily Anakineticinae which is erected for those Australian and New Zealand genera formerly included in the Magadinae.

WITH the exception of the Terebratellidae (subfamilies Terebratellinae, Anakineticinae nov., Bouchardiinae and Magadinae), Cainozoic articulate brachiopod families are cosmopolitan in distribution. Cainozoic members of the Terebratellidae are unknown in the northern and western hemispheres but are the principal components of the Recent brachiopod faunas in Australia, New Zealand, South America and Antarctica. In these areas, brachiopods are not rare members of the benthos, as they appear to be in other parts of the world.

The subfamily Anakineticinae nov. is an exclusively southern subfamily which apparently evolved in the biogenic sands of New Zealand and Australia during the Oligocene and Miocene. In New Zealand, a drastic reduction in the extent of shallow marine shelf environments by Late Miocene time (MacKinnon 1987) resulted in the disappearance of brachiopods specialised for these regimes, and both anakineticinid genera from that area (*Magadina*, *Rhizothyris*) are now extinct. In contrast, the stability of the Australian region has provided a virtually continuous record (Eocene to Recent) of anakineticinids specialised for bryozoan sands. Present day communities living in the bryozoan sands of the Australian shelf replicate those found in the Tertiary bryozoan sands, and the two communities are sometimes found in juxtaposition, as in southern Victoria, for example, where cliffs of the Aire coast border shelf waters.

Living anakineticinid species have been described in a series of papers (see Richardson 1987) which show that they are widely distributed in relation to latitude, longitude and depth, and that they possess a variety of adaptations for life in shifting bryozoan sands. These species have given a new insight into the struc-

ture and function of the pedicle, showing that it is not analagous to a stalk or stem but is a variable appendage used either to tether or to move individuals in soft sediments. Differences in the pedicle system and therefore in substrate relationships are reflected in overall shape and size, as well as in the beak and cardinalia.

Erection of a new subfamily for the Australian and New Zealand genera previously included in the Magadinae leaves the latter subfamily with four European Cretaceous genera, three of which are little known. The Australasian genera have been transferred to the Anakineticinae because they differ from *Magas*, the type genus of the Magadinae, in distribution of thickening, beak type, and in the form of the posterior surface of the cardinal process. The distribution of thickening in *Magas* indicates that the dorsal valve would have been uppermost in life and the ventral valve in contact with the underlying substrate (chalk), in contrast with the opposite orientation of austral genera. The posterior surface of the cardinal process of *Magas* is small and cup-shaped whereas in the genera attributed to the Anakineticinae it is prominent and distinctive in shape, with lateral vertical or near-vertical wings flanking a median horizontal surface (trefoil). Steinich (1968) and Johansen (1987) have remarked on the similarities between *Magas chitoniformis* and *Dalliglas nobilis* (Dallinidae) which they can separate only on the composition of the loop and density of punctae. Both *Magas* and *Dalliglas* exhibit adult loops at an early stage of the developmental sequence which is characteristic of terebratellacean families (Richardson 1975). Family position can be determined only from the patterns of resorption evident in intermediate stages, not from early or late stages of development. Adult

loop pattern therefore does not define the family position of *Magas* which may prove to be a member of the Dallinidae

Discussion of the evolutionary derivation of members of the Anakineticinae will be included in a forthcoming paper on Australian Terebratellidae.

The material described herein is housed in the collections of the South Australian Museum (SAM), the Western Australian Museum (WAM), and the Museum of Victoria (NMV).

SYSTEMATICS

Superfamily TEREBRATELLACEA King, 1850

Family TEREBRATELLIDAE King, 1850

Subfamily ANAKINETICINAE nov.

Diagnosis. Posteriorly thickened smooth Terebratellidae with permesothyrid foramen; cardinalia consisting of socket ridges, crural bases, and a cardinal process with trefoil posterior surface.

Genera included. *Anakinetica* Richardson, 1987; *Adnatida* nov.; *Aliquantula* nov.; *Australiarcula* Elliott, 1959; *Elderra* nov.; *Magadina* Thomson, 1915; *Magadinella* Thomson, 1915; *Parakinetica* Richardson, 1987; *Pilkena* nov.; *Pirothyris* Thomson, 1927; *Rhizothyris* Thomson, 1915.

Distribution. Cretaceous–Recent; Australia, New Zealand.

Comments. All anakineticinid genera are posteriorly thickened with a permesothyrid foramen. They differ from one another primarily in the cardinalia: in the extent of thickening of the hinge platform, in the presence of hinge pits or of a hinge trough and, if the latter is present, in its extent.

Differential thickening is a reliable indicator of free life in living forms and a permesothyrid foramen of an inert, non-muscular pedicle (Richardson 1981a); i.e. individuals that are pediculate but are neither tethered nor fixed to the underlying substrate. The presence of a hinge trough or of pits is associated with different actions of the pedicle (Richardson 1987). In the former, the action of pedicle muscles rotates the pedicle or the shell (depending on the mass of substrate bonded with the pedicle); in the latter they push the pedicle in and out of its housing, the beak. Rotatory action is associated with a bonded pedicle and attachment of the dorsal pedicle muscles to a hinge trough. In/out action is associated with a free pedicle and attachment

of dorsal adjustor muscles to a pair of posterior hinge pits.

A hinge trough is characteristic of four of the genera and may (1) extend the full length of the platform (*Magadina*), (2) be restricted to its anterior section as a result of enlargement of the inner socket ridges and cardinal process (*Magadinella*, *Elderra*), or (3) be restricted to its posterior region (*Aliquantula*) by enlargement of the crural bases. Genera with hinge pits may differ in the position of the hinge platform relative to the valve surface and in shell shape and beak form, differences which, in members of living genera (*Anakinetica*, *Parakinetica*), are related to direction of movement and to the disposition of the pedicle processes.

Neither hinge trough nor pits are evident on the hinge platform of species of *Adnatida*. The absence of any area for attachment of the dorsal pedicle adjustor muscles is a likely indicator of atrophy or loss of the pedicle system, as are the small foramen and incurved beak also seen in these species. They would have been free-lying forms without any capacity to move and similar to some of the populations of *Neothyris lenticularis* described by Chapman & Richardson (1981) and Richardson (1981b). Species within each genus are distinguished on consistent differences in size and shape, on loop pattern, and on details of the hinge platform. Loop pattern is linked with the space available within the mantle cavity. In shells of small size and heavy thickening (*Magadina*, *Anakinetica recta*) the adult loop is at an early stage in the developmental sequence; i.e. with a ventral ring and wide descending branches separately attached to a high median septum. A long reflected loop without septal attachments is found in *Aliquantula* and *Elderra*, genera of moderate size and having the hinge platform smaller in relation to valve area than in *Anakinetica* and *Magadinella*. The loop is rarely recovered in its entirety but its parts and their relationship are evident during dissection.

Several Japanese species are difficult to distinguish from Australian anakineticinids. The Miocene species *Tanakura tanakura* Hatai, 1936, for example, was included by me (Richardson 1987) in the Magadinae because of its similarity to species of *Anakinetica*. The Pliocene–Recent species *Nipponithyris nipponensis* Yabe & Hatai, 1934 is also very similar to *Aliquantula insolita*. However, the adult loop of *N. nipponensis* displays double lateral connecting bands (Richardson 1975), showing that it is a member of the Dallinidae. The development

and adult loop of *T. tanakura* are unknown but the short median septum carries no evidence of connecting bands, indicating that a long reflected loop would have been present. Since a loop of this type is found as the ultimate developmental stage in all families and, since no other members of the Terebratellidae have been described from Japan, it is possible that *Tanakura* is also a dallinid genus, and the similarities in shape, size, beak and cardinalia are thus considered homeomorphies resulting from the occupation of sediments of similar type. Hatai (1940) described *T. tanakura* from coarse grained sandstones consisting of fragments of marine organisms and *N. nipponensis* from a shelf substrate of sand and shell fragments.

Genus *Anakinetica* Richardson, 1987

Type species. Terebratella(?) Cumingii Davidson, 1852 from the Recent of Australia.

Other species. Terebratula compta Sowerby, 1845; *A. breva* sp. nov.; *A. recta* sp. nov.; *A. tumida* sp. nov.

Occurrence. Australia; Oligocene to Recent.

Diagnosis. Sulcate. Beak suberect to straight; beak ridges sharp; symphytium wide, flat; cardinal margin straight or nearly straight. Hinge platform with posterior pits for attachment of dorsal adjustor muscles. Loop with ascending

and descending branches separate or fused and with lateral connecting bands.

Comments. Species of *Anakinetica* lack a hinge trough for attachment of the dorsal adjustor muscles. The solid hinge platform, formed by fusion of the socket ridges, crural bases, and the anterior surface of the cardinal process (Richardson 1987), contains two pits which flank the posterior surface of the cardinal process. In the living species *A. cumingii* and also in *Parakinetica stewarti*, these pits serve as the sites of attachment of the dorsal adjustor muscles, and it is inferred that the pedicle of all fossil species included in the genus likewise would have been free and would have functioned in similar ratchet-like fashion.

Species of *Anakinetica* differ externally in size, outline, beak length, curvature of the cardinal margin, and in strength of sulcation. Internally they differ in the length and height of the septum, stage of loop development, and in details of the hinge platform. Two of these features appear to be linked. A short septum and a more advanced loop stage (with thin lateral connecting bands) are found in *A. compta* and *A. breva*. A long septum and wide connecting bands occur together in *A. tumida* and *A. recta*. The components of the hinge platform are fused but identifiable in *A. breva* and *A. tumida* but are not identifiable in *A. compta* and *A. recta*.

Key to species of *Anakinetica*

(based on external features only)

1. Beak length $< 0.2 \times$ valve length *A. breva*
- Beak length $> 0.2 \times$ valve length 2
2. Cardinal margin curved, beak straight *A. recta*
- Cardinal margin straight or nearly straight, beak suberect 3
3. Outline trapezoid, greatest width posterior to mid-length .. *A. tumida*
- Outline ovate, greatest width at mid-length; anterior commissure strongly sulcate *A. compta*

Anakinetica compta (Sowerby in Strezlecki, 1845)

Type material. See comments.

Fig. 1A–F

Terebratula compta Sowerby in Strezlecki 1845: 297, pl. 19, fig. 4

Terebratella compta.—Tenison-Woods 1865: 2, pl. 2, fig. 4a–c.

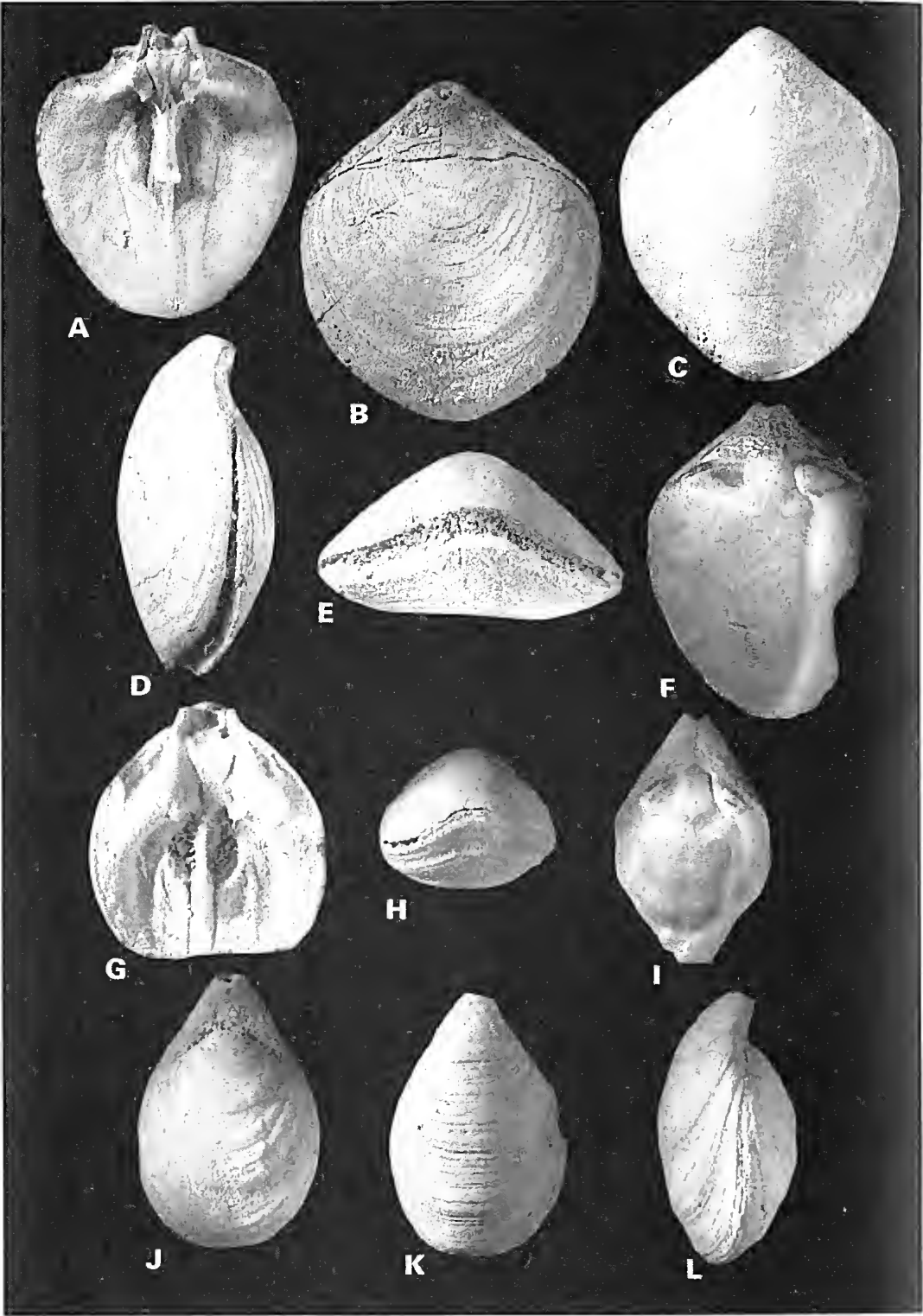
non *Terebratella compta*.—Etheridge 1876: 19–20, pl. 2, fig. 5a–d [= *Magadinella woodsiana* (Tate, 1880)].

non *Magasella compta*.—Tate 1880: 162–163, pl. 10, fig. 6a–e [= *A. breva* sp. nov.].

Magadina compta.—Thomson 1915: 399, fig. 10

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P86974	18.8	15.0	14.9	8.9
NMV P3748	19.3	14.8	14.8	9.0
NMV P86973	17.9	13.6	12.9	8.9
NMV P58903	17.8	13.6	13.8	8.9
NMV P134239	18.5	14.9	15.5	8.2



Description. Outline subquadrate, greatest width at or slightly posterior to mid-length; dorsal valve with flattened umbo; anterior commissure deeply and narrowly sulcate. Beak suberect; cardinal margin straight; symphytium wide, flat to gently concave. Hinge platform wedge-shaped, almost square with indented posterior margin; surface relief low; posterior surface of cardinal process large, lateral surfaces lining posteriorly projecting socket ridges. Medium septum thick, low, terminating mid-length of valve. Loop with thin lateral connecting bands. Hinge teeth triangular in outline. Beak interior and lateral walls heavily thickened, leaving round tunnel for pedicle.

Comments. Sowerby (in Strezlecki 1845) described *Terebratula compta* on the basis of specimens collected from "an elevated beach at Port Fairy" on the Cape Otway coast, Victoria. Tate (1880) noted that "Strezlecki mistook our Older Tertiary deposits for Post Tertiary beaches". Port Fairy (if considered as synonymous with Point Fairy) contains no Tertiary outcrops although they occur inland in this general area. In 1865, Tenison-Woods referred specimens collected at Mount Gambier and Portland to *T. compta* and his figures agree with those of Sowerby. The Natural History Museum, London, where some of Sowerby's material is deposited, has no record of *T. compta*. The specimens described and figured herein were collected from the Mount Gambier Limestone (Janjukian, Upper Oligocene) at Portland, Victoria. Since no problem exists in the identification of Sowerby's species, and in accordance with Article 75 (b)(ii) of the International Code of Zoological Nomenclature, it is not considered necessary to designate a neotype.

Anakinetica recta sp. nov.

Fig. 1G-L

Name. From Latin *rectus* (straight), in reference to the beak.

Type material. Holotype WAM 90.241 and paratypes WAM 90.242-90.246, NMV P134722, from Frank Paulik's Bore (Lot 6, depth unknown), Jandakot, Western Australia.

Other horizons and localities. Western Australia. Jandakot: Adrian's Nursery Bore at 38.4 to 39.3 m; Schafer's Bore (Lot 415) at 40.6 m; Cement Works Bore at 33.6 to 33.7 m; Poletti's Bore No. 2 (Lot 7) at 39.6 to 41.1 m; Gnaranga Bore No. 8 at 77.8 m. Gonnells: Kowalski's Bore (Lot 1) at 28.4 to 29.6 m. All material cited is housed in the Western Australian Museum.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
WAM 90.241	9.9	8.1	7.7	4.8
WAM 90.242	9.1	7.6	6.6	4.8
WAM 90.243	9.3	7.2	6.1	4.8
WAM 90.244	9.1	7.7	6.6	5.0
NMV P134722	8.9	6.9	6.4	3.7

Description. Outline elongate-ovate with greatest width at mid-length. Beak straight, symphytium slightly concave, cardinal margin curved. Hinge platform outline trapezoidal; posterior ends of socket ridges blunt, projecting slightly beyond posterior margin of valve; boundaries of components of platform not identifiable. Median septum extending slightly beyond mid-length of valve, high anteriorly. Loop with ascending and descending branches separate, attachments to septum wide. Hinge teeth triangular in outline. Lateral walls and beak interior heavily thickened, leaving round tunnel for pedicle.

Comments. Dr G. Kendrick (pers. comm.), Western Australian Museum, considers the age of the bores to be Pliocene to Early Pleistocene.

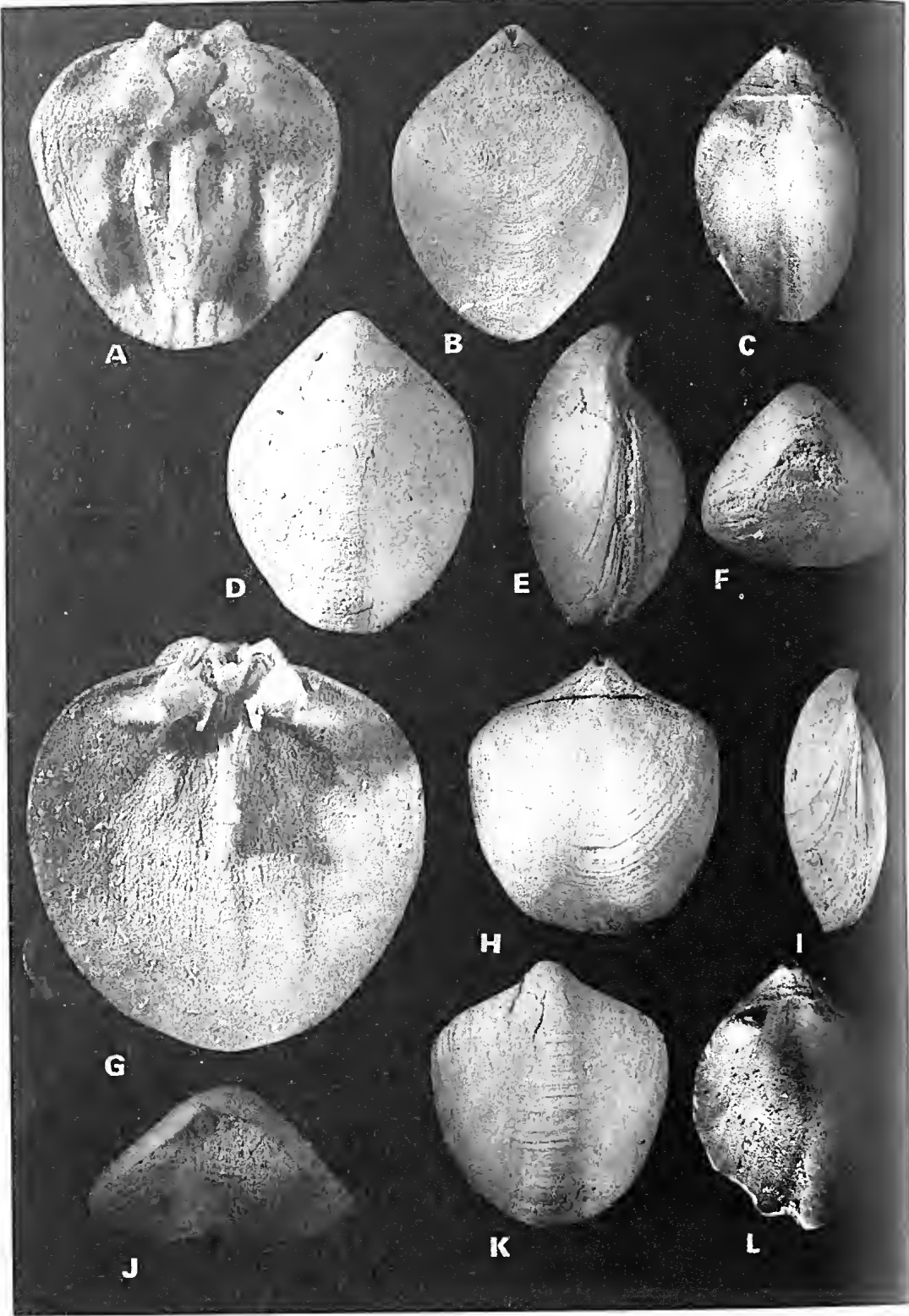
Anakinetica tumida sp. nov.

Fig. 2A-F

Name. From Latin *tumidus* (swollen), in reference to the cardinalia.

Type material. Holotype NMV P17329 and paratypes NMV P17330, P17331, P134203-P134207, from the Brighton Sands, Cheltenham Member (Cheltenhamian, Pliocene), Beaumaris, Victoria.

←
Fig. 1. A-F, *Anakinetica compta* (Sowerby, 1845). A, NMV P86984, dorsal interior, $\times 2.5$. B-E, NMV P86974, dorsal, ventral, lateral, anterior (ventral valve uppermost) views, $\times 2.5$. F, NMV P134202, ventral interior, $\times 2.5$. G-L, *Anakinetica recta* sp. nov. G, paratype WAM 90.245, dorsal interior, $\times 5$. H, J-L, holotype WAM 90.241, anterior (ventral valve uppermost), dorsal, ventral, and lateral views, $\times 4$. I, paratype WAM 90.246, ventral interior, $\times 4$.



Measurements. (In mm).

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17329	16.8	13.2	12.4	9.2
NMV P17203	16.6	13.2	11.6	7.9
NMV P17204	17.1	13.4	12.4	9.2
NMV P17205	15.1	12.0	11.4	7.8
NMV P17206	15.0	11.9	10.8	8.1
NMV P17207	16.3	12.9	11.9	8.6

Description. Outline trapezoidal with greatest width posterior to mid-length; unequally biconvex, ventral valve deeper than dorsal valve, with median carina and steep lateral slopes; dorsal valve with flattened umbo and shallow median sulcus; anterior commissure narrowly sulcate. Beak suberect; cardinal margin straight; symphytium wide. Hinge platform outline trapezoidal; socket ridges, crural bases and anterior surface of cardinal process fused but identifiable. Median septum long, high anteriorly. Loop with ascending and descending branches having separate attachments to septum. Hinge teeth triangular in outline. Beak interior and lateral walls heavily thickened, leaving round tunnel for pedicle.

Comments. *A. tumida* closely resembles the Recent species *A. cumingii*. In *A. tumida* the cardinal margin is typically straight and variants with a slightly curved margin are rare, whereas the cardinal margin of *A. cumingii* varies from slightly to moderately curved. The ventral valve of *A. tumida* is always more strongly convex than the dorsal valve; in *A. cumingii* the valves are commonly equal in biconvexity. Fusion of the elements of the cardinalia appears to occur at a later stage in *A. tumida* than in *A. cumingii*; one dorsal valve of the former, 9 mm in length, exhibits medial fusion of the crural bases but not with the anterior surface of the cardinal process, so that a small posterior hinge trough is present at this stage.

Anakinetica breva sp. nov.

Fig. 2G-L

Magasella compta.—Tate 1880: 162–163, pl. 10,fig. 6a–e [non *Anakinetica compta* (Sowerby in Strezelecki, 1845)].*Name.* From Latin *brevus* (short), in reference to the beak length.*Type material.* Holotype NMV P17348, paratypes NMV P17349, P17350, P134213–P1234216, from the Point Addis Limestone (Janjukian, Upper Oligocene), Aireys Inlet, Victoria.*Other horizons and localities.* South Australia. Mannum Formation (Lower Miocene): River Murray cliffs at Mannum. Victoria. Fyansford Formation (Longfordian, Lower Miocene): North Belmont Quarry, Geelong. Puebla Formation (Longfordian Lower Miocene): Jan Juc Point, mouth of Spring Creek, Torquay. Scutellina Limestone (Longfordian, Lower Miocene): Jan Juc, Torquay. All material cited is housed in the Museum of Victoria.*Measurements.* (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17348	18.0	15.8	14.9	9.1
NMV P134213	18.6	15.5	15.6	9.7
NMV P134214	17.7	15.6	16.0	9.4
NMV P134215	17.4	15.4	14.4	9.0
NMV P134216	16.1	14.0	12.8	8.6

Description. Outline ovate, greatest width slightly posterior to mid-length. Dorsal valve almost plane, umbo flattened with median sulcus. Anterior commissure deeply and narrowly sulcate. Beak suberect; cardinal margin straight. Hinge platform short, length approximately 3 mm in dorsal valve 15 mm long; outline trapezoidal; anterior surface of cardinal process prominent, fused dorsally. Median septum short, terminating posterior to mid-length. Loop with thin lateral connecting bands. Hinge teeth triangular in outline. Lateral walls and beak interior moderately thickened.

Magadinella Thomson, 1915*Type species.* *Magasella Woodsiana* Tate, 1880 from the Upper Oligocene to Middle Miocene of Australia.*Other species.* *M. mineuri* Richardson, 1987; *M. hamiltonensis* sp. nov.

Fig. 2. A–F, *Anakinetica tumida* sp. nov. A, paratype NMV P17330, dorsal interior, $\times 4$. B, D–F, holotype NMV P17329, dorsal, ventral, lateral, and anterior (ventral valve uppermost) views, $\times 3$. C, paratype P17331, ventral interior, $\times 3$. G–L, *Anakinetica breva* sp. nov. G, paratype NMV P17349, dorsal interior, $\times 4$. H–K, holotype NMV P17348, dorsal, lateral, anterior (ventral valve uppermost) and ventral views, $\times 2.25$. L, paratype NMV P17350, ventral interior, $\times 2.5$.

Occurrence. Australia; Upper Oligocene, Miocene, Recent.

Diagnosis. Sulcate. Beak erect to nearly straight; beak ridges sharp; symphytium wide; hinge line slightly to strongly curved. Hinge platform with shallow hinge trough, variable in size; cardinal process with swollen anterior process. Loop with ascending and descending branches fused anteriorly.

Comments. The diagnosis of the genus given by Richardson (1987) has been slightly modified following study of the two Tertiary species. The beak of the Recent species *Magadinella mineuri* is one-fifth to one-sixth the shell length, the symphytium is slightly concave without a median ridge, the cardinal margin is strongly curved, and the cardinalia occupy approximately one-third to one-quarter the length of the dorsal valve. In size and convexity *M. mineuri* and *M. woodsiana* are similar, but the cardinal margin of *M. woodsiana* may be slightly to strongly curved, a median ridge is variably developed on the symphytium, and the hinge platform is shorter relative to dorsal valve length. *M. hamiltonensis* is smaller, not heavily thickened, and the beak, hinge platform, and septum are all shorter than in the other two species.

Magadinella woodsiana (Tate, 1880)

Fig. 3A–F

Magasella Woodsiana Tate 1880: 163–164, pl. 10, fig. 3a–d.—Tate 1899: 256–257.

Magasella compta.—Pritchard 1896: 142–143 [partim., non *Anakinetica compta* (Sowerby in Strezlecki, 1945)].

Magadinella woodsiana.—Thomson 1915: 400–402, fig. 13a–c.—Thomson 1927: 277–278, fig. 92a–c.

Type material. Syntypes SAM T886A–K, M, N, from Morrundi, River Murray, South Australia. Horizon unknown.

Other horizons and localities. South Australia. Mount Gambier Limestone (Janjukian, Upper Oligocene); Mount Gambier. Victoria. Calder River Limestone (Janjukian, Upper Oligocene); Wilks' Localities 3 and 4, Aire coast. Point Addis Limestone (Janjukian, Upper Oligocene); Point Addis; Aireys Inlet; Kewarren. Sandford Limestone (Janjukian, Upper Oligocene);

quarry on south side of Runymede Road, Sandford. All material cited is housed in the Museum of Victoria.

Measurements. (In mm; specimens from the Point Addis Limestone.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17341	21.8	18.6	17.2	11.2
NMV P134223	18.0	14.0	12.1	9.9
NMV P134224	18.4	15.0	12.4	10.8
NMV P134225	17.1	14.7	11.2	11.1
NMV P134226	19.2	15.6	10.9	10.0
NMV P134227	17.4	13.9	11.5	9.8

Description. Outline variable, pyriform to ovate (narrowly to broadly) with maximum breadth at mid-length or farther forward; moderately to strongly biconvex. Beak nearly straight to sub-erect, one-quarter to one-eighth ventral valve length; symphytium flat to slightly concave, median longitudinal ridge variably developed; cardinal margin slightly to strongly curved. Hinge platform with hinge trough between medial borders of fused crural bases and socket ridges; cardinal process anterior surface variable in size, confined to posterior area or extending to posterior border of platform, not fused dorsally. Septum low, blade-like anteriorly, crest rounded posteriorly. Loop with ascending and descending branches fused anteriorly, separate posteriorly.

Comments. *M. woodsiana* is found in greatest abundance in the Point Addis Limestone. The preceding description is based on examination of hundreds of specimens from a single horizon and supplements Tate's description of the species from Morrundi, an area from which additional material is probably not obtainable.

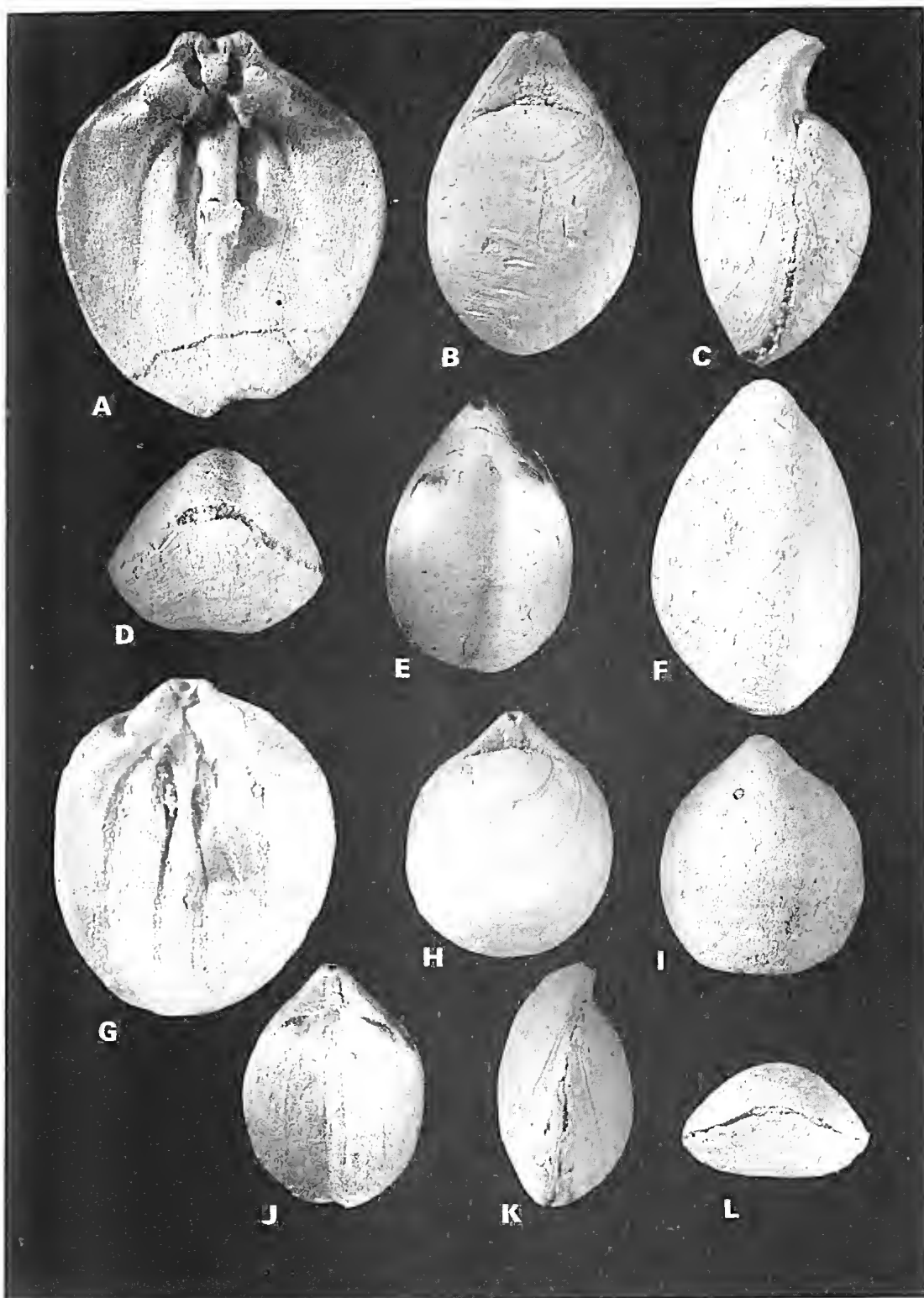
Magadinella hamiltonensis sp. nov.

Fig 3G–L

Name. From the type locality.

Type material. Holotype NMV P134228 and paratypes NMV P134229–P134233, P134241, P134242, from the Muddy Creek Marl (Balcombian, Middle Miocene), Muddy Creek, Hamilton, Victoria.

Fig. 3. A–F, *Magadinella woodsiana* (Tate, 1880). A, NMV P134210, dorsal interior, $\times 3.5$. B–D, F, NMV P17341, dorsal, lateral, anterior (ventral valve uppermost) and ventral views, $\times 2.5$. E, NMV P134211, ventral interior, $\times 2.25$. G–L, *Magadinella hamiltonensis* sp. nov. G, paratype NMV P134229, dorsal interior, $\times 5.5$. H, I, K, L, holotype NMV P134228, dorsal, ventral, lateral and anterior (ventral valve uppermost) views, $\times 3.4$. J, paratype P134230, ventral interior, $\times 3.4$.



Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P134228	11.0	9.0	8.6	5.6
NMV P134231	10.3	8.9	8.6	5.6
NMV P134232	10.1	8.7	8.6	5.4
NMV P134230	10.7	8.9	8.2	5.7
NMV P134241	9.3	7.8	7.4	4.8
NMV P134242	8.4	7.6	6.5	3.9

Description. Outline ovate; moderately biconvex. Anterior commissure slightly sulcate. Beak nearly straight, approximately one-fifth of valve length; symphytium slightly concave with median longitudinal ridge; cardinal margin gently curved. Hinge platform with wide, shallow hinge trough; anterior surface of cardinal process slightly variable in size, not extending beyond posterior half of platform. Septum extending to mid-length of valve, high anteriorly. Loop with ascending and descending branches fused anteriorly.

Elderra gen. nov.

Name. From the Aboriginal (handsome). Gender feminine.

Type species. *Elderra toorlooensis* sp. nov. from the Miocene of Australia.

Diagnosis. Sulcate. Beak suberect, beak ridges sharp; symphytium with median and lateral ridges; cardinal margin curved. Hinge platform with hinge trough. Loop without septal connecting bands.

Comments. *Elderra* contains only one species which is similar in many features to variants of species included in *Magadinella*, but which is notably less variable in size, shape, beak characters, and in the extent of thickening of the cardinalia. Essential distinguishing features are the loop stage and the ridges which demarcate the borders of the symphytium.

Elderra toorlooensis sp. nov.**Fig. 4A-F**

Name. From the type locality.

Type material. Holotype NMV P17351 and paratypes NMV P17352, P17353, P86845, P134217-P134220, from the Gippsland Limestone, Bairnsdale Limestone Member (Bairnsdalian, Middle Miocene), Toorloo Creek, Lakes Entrance, Victoria.

Other horizons and localities. Victoria. Gippsland

Limestone, Wuk Wuk Marl Member (Batesfordian-Bairnsdalian, Lower-Middle Miocene): lower beds, Skinner's; lower and upper beds, Drier's. Gippsland Limestone, Bairnsdale Limestone Member (Bairnsdalian, Middle Miocene): Pound Swamp; shaft on Rosehill Farm. Tambo River Formation (Mitchellian, Upper Miocene): cliffs on left bank of Tambo River, Swan Reach; cutting near Toorloo Arm. Unknown Tertiary formation: oil shaft dump, Lakes Entrance. All material cited is housed in the Museum of Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P17351	33.1	29.0	25.9	16.8
NMV P134217	29.8	25.7	22.7	16.3
NMV P134218	31.1	27.2	22.6	15.7
NMV P134219	19.8	26.2	22.5	15.1
NMV P134220	29.5	25.1	21.0	17.7

Description. Outline ovate, biconvex. Anterior commissure gently sulcate. Symphytium slightly concave, with median ridge and lateral ridges at junctions of symphytium and palintropes. Hinge platform trapezoidal in outline; socket ridges projecting posteriorly beyond umbo as two pointed processes, fused anteriorly with swollen crural bases; hinge trough extending length of platform, deeper posteriorly; cardinal process with slightly bulbous anterior surface. Septum short, base thick, crest sharp.

Comments. Little morphological variation is evident in specimens from the environs of Toorloo Creek and the Tambo and Mitchell Rivers. The specimens collected from an oil shaft dump at Lakes Entrance are smaller in size and slightly narrower in outline with stronger curvature of the cardinal margin, features which alone do not justify taxonomic separation.

Adnatida gen. nov.

Name. From the Latin *adnatus* (united), in reference to the components of the cardinalia. Gender feminine.

Type species. *Magasella deformis* Tate, 1880 from the Eocene of Australia.

Other species. *A. gnangarensis* sp. nov.

Diagnosis. Sulcate. Beak pointed, erect, foramen small; symphytium concave; beak ridges and cardinal margin curved. Hinge platform heavily thickened without hinge trough or pits, with posterior surface of cardinal process only identifiable structure.

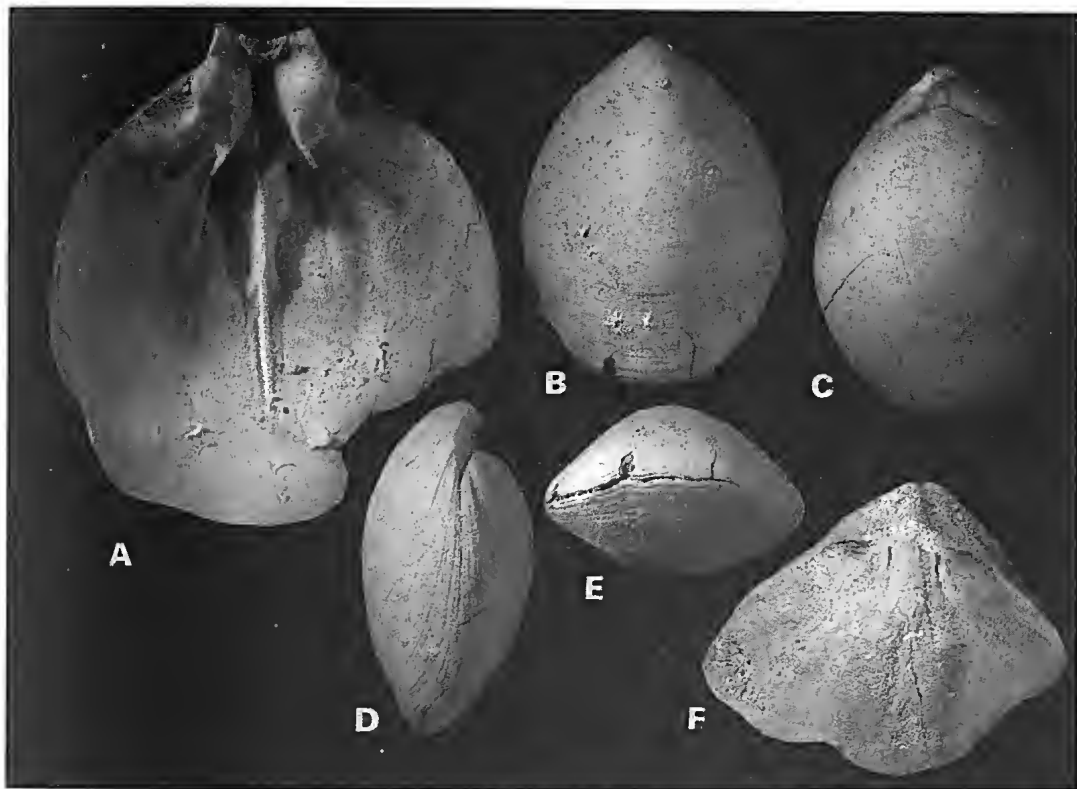


Fig. 4. A-F, *Elderra toorlooensis* sp. nov. A, paratype NMV P17352, dorsal interior, $\times 2.6$. B-E, holotype NMV P17351, dorsal, ventral, lateral and anterior (ventral valve uppermost) views, $\times 1.25$. F, paratype NMV P17353, ventral interior $\times 1.7$.

Comments. The heavily thickened hinge platforms of the two species included in *Adnatida* appear to contain no sites for muscle attachment other than the posterior surface of the cardinal process (attachment surface of the diductor muscles). The absence of a hinge trough or pits, together with the small erect beak and tiny foramen, are indicators of an atrophied pedicle system and a free-lying existence. The appearance of the hinge platform suggests that a life-style characteristic of species of *Anakinetica* would have preceded loss of pedicle function in the species of *Adnatida*.

The species of *Adnatida* may be differentiated externally by the curvature of the cardinal margin (moderate in *A. deformis*, strong in *A. gnangarensis*), degree of sulcation (moderate in *A. gnangarensis*, strong in *A. deformis*), shape (broadly ovate in *A. deformis*, pyriform in *A. gnangarensis*) and in the pronounced convexity of the dorsal valve of *A. deformis*. The loop of neither species has been preserved, but the condition of the septum suggests that the loop of *A.*

deformis would show ascending and descending branches, whereas that of *A. gnangarensis* would have fused branches with thin, lateral connecting bands.

Adnatida deformis (Tate, 1880)

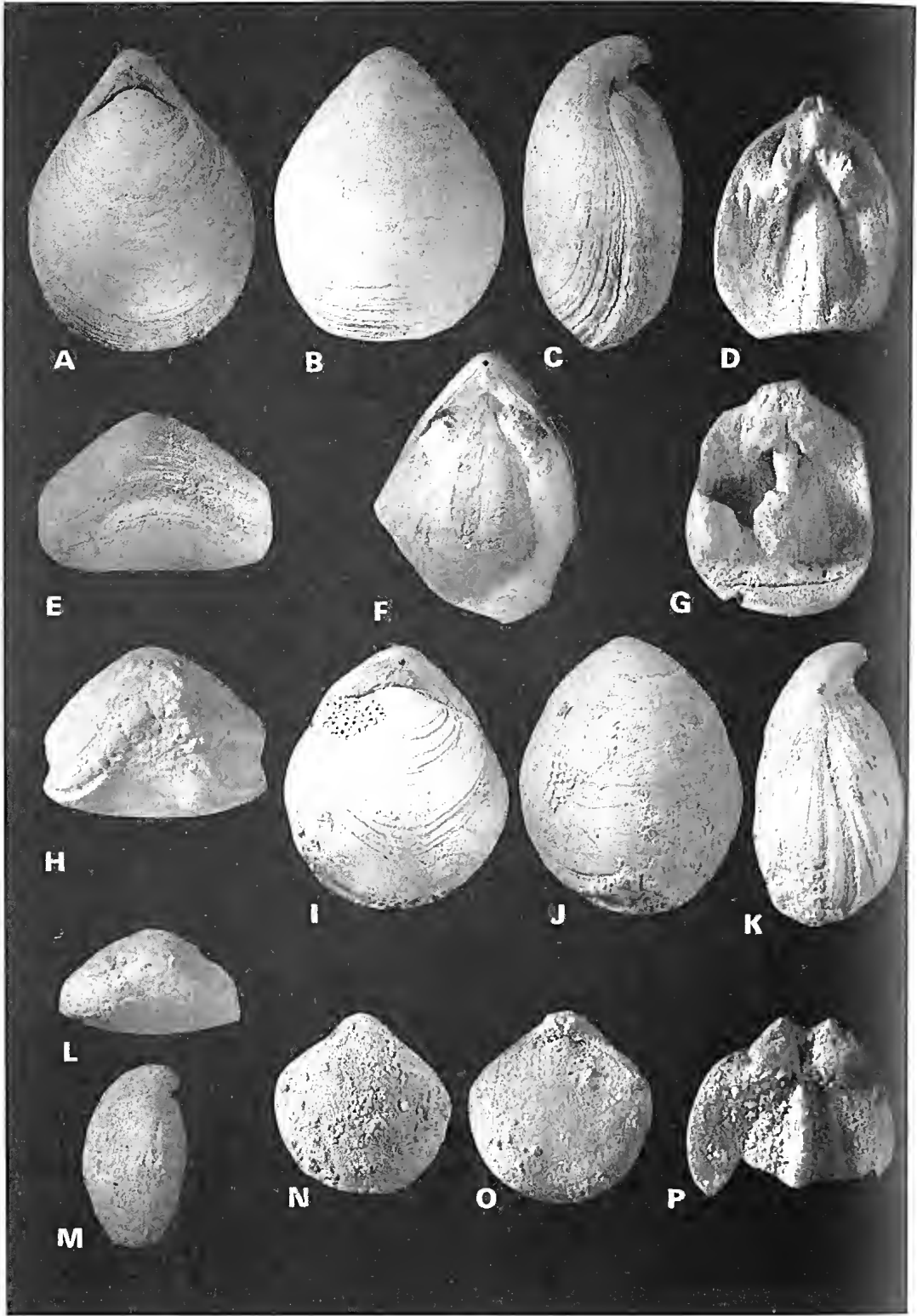
Fig. 5G-K

Magasella deformis Tate 1880: 165-166, pl. 10, fig. 5a-c.

Magadina(?) deformis.—Thomson 1927: 267.

Type material. Five syntypes, SAM T888A-E, from the Tortachilla Limestone (Eocene), Maslin Bay, Aldinga, South Australia.

Description. Length of figured specimen (Fig. 5H-K) 11.7 mm, breadth 9.2 mm, depth 6.6 mm. Strongly sulcate. Outline broadly ovate, greatest width just anterior to mid-length. Symphytium slightly concave; cardinal margin slightly curved. Hinge platform almost circular in outline; posterior surface of cardinal process roughened, slightly lower than surrounding plat-



form. Septum terminating anterior to mid-length, high anteriorly, posterior segment with blunt crest. Loop unknown.

***Adnatida gnangarensis* sp. nov.**

Fig. 5A–F

Name. From the type locality.

Type material. Holotype WAM 90.247 and two paratypes WAM 90.248, 90.249 from the Western Australian Mines Department Bore No. 5, 44.2 to 46.3 m (Pliocene to Lower Pleistocene), Gnangara, Western Australia.

Description. Length of holotype 18.1 mm, breadth 13.4 mm, depth 9.0 mm. Moderately sulcate. Outline pyriform, greatest width just anterior to mid-length. Symphytium concave, cardinal margin strongly curved. Hinge platform outline elongately triangular; cardinal process with lateral segments of posterior surface incurved, rim and presumed anterior surface elevated above surrounding fused elements; anterior border indented at union with septum. Septum terminating anterior to mid-length, crest blade-like. Loop unknown.

***Magadina* Thomson, 1915**

Type species. *Magadina browni* Thomson, 1915 from the Miocene of New Zealand.

Other species. *M. clifdenensis* Finlay, 1924; *M. thomsoni* Finlay, 1924; *M. waipariensis* Thomson, 1915; *Magasella lunata* Tate 1899.

Occurrence. Australia, New Zealand; Oligocene–Miocene.

Comments. Thomson's diagnoses (1915, 1927) included Australian species now referred to *Anakinetica* (*compta*, *cumingii*), *Bouchardiella* (*cretacea*), and *Parakinetica* (*deformis*). The only Australian species now included in the genus is *M. lunata*. *Magadina* is distinguished from other members of the subfamily in the presence of a deep hinge trough extending the full length of the platform, and in the absence of any medial fusion of the crural bases and/or the anterior surface of the cardinal process.

***Magadina lunata* (Tate, 1899)**

Fig. 5L–P

Magasella lunata Tate 1899: 256, pl. 8, fig. 3, 3a. (?) *Magadina lunata*.—Thomson 1927: 276.

Type material. Holotype SAM T1724A from Croydon Bore at 122 to 375 m (Miocene), Adelaide, South Australia.

Other horizon and locality. South Australia. Mannum Formation (Lower Miocene); quarry at Mannum. Material housed in the Museum of Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
SAM T1724A	7.1	6.3	6.9	3.8
NMV P134235	6.9	5.7	7.2	4.1
NMV P134236	7.2	6.1	7.0	4.3
NMV P134237	7.1	6.2	6.6	4.3
NMV P134238	5.6	4.8	6.2	2.8

Description. Outline nearly circular; unequally biconvex, dorsal valve nearly plane. Anterior commissure broadly sulcate. Beak suberect, short; deltidial plates conjunct; cardinal margin slightly curved. Hinge platform wide, short; crural bases and socket ridges fused, hinge trough wide, deep; cardinal process small, not projecting into hinge trough. Septum terminating just anterior to mid-length of valve, high anteriorly. Loop with ascending and descending branches separate.

Comments. The Tate Collection in the Department of Geology, University of Adelaide, contains a card with five specimens (T1724A–E) labelled *Magasella lunata*. Only one of these specimens, T1724A, possesses all the external features described and figured by Tate (1899). This specimen is plano-convex with anterior sulcation, a permesothryd foramen, fused concave deltidial plates, and a curved cardinal margin. The remaining specimens are also plano-convex and sulcate but they display different beak characters (a hypothryd foramen, rudimentary deltidial plates, and a nearly straight cardinal

Fig. 5. A–F, *Adnatida gnangarensis* sp. nov. A–C, E, holotype WAM 90.247, dorsal, ventral, lateral and anterior (dorsal valve uppermost) views, $\times 2.5$. D, paratype WAM 90.248, dorsal interior $\times 2.5$. F, paratype WAM 90.249, ventral interior, $\times 2.5$. G–K, *Adnatida deformis* (Tate, 1880). G, NMV P134212, dorsal interior, $\times 3.5$. H–K, NMV P134240, anterior (ventral valve uppermost), dorsal, ventral and lateral views, $\times 3.5$. L–P, *Magadina lunata* (Tate, 1899). L–O, NMV P134235, anterior (ventral valve uppermost), lateral, ventral and dorsal views, $\times 4$. P, NMV P87579, dorsal interior, $\times 5$.

margin) and were referred to *Malleia portlandica* by Richardson (1973b). The above description of the species is based on specimens collected in the Mannum Formation.

M. lunata is smaller in size than the New Zealand species. The largest specimen of *M. lunata* is 7.2 mm in length; the largest specimen of *M. browni* from the Museum of Victoria's collection is 13.3 mm. *M. lunata* resembles *M. cliffdenensis* in beak and cardinal margin, both of which are shorter than in *M. browni*. The hinge platform of *M. lunata* differs from that of New Zealand species in its greater width and in the socket ridges, which are less strongly convergent and project beyond the margin of the valve for approximately half their lengths.

Pilkena gen. nov.

Name. From the Aboriginal *pilkena* (different). Gender feminine.

Type species. *Pilkena compressa* sp. nov. from the Oligocene of Australia.

Diagnosis. Sulcate. Beak nearly straight, beak ridges sharp; symphytium with low median ridge; cardinal margin slightly curved. Hinge platform with posterior pits for attachment of dorsal adjustor muscles. Loop long, reflected, without septal connecting bands.

Comments. The hinge platform of *Pilkena* is similar to that of *Anakinetica* in the absence of a hinge trough and the presence of posterior pits for attachment of the dorsal adjustor muscles. *Pilkena* is distinguished from *Anakinetica* by the more advanced loop and by the position of the hinge platform relative to the valve surface. The hinge platform of *Pilkena* does not extend beyond the margin of the dorsal valve, so that the tip of the dorsal umbo is visible. In addition, the posterior surface of the cardinal process is steeply inclined, and consequently both the posterior surface and the posterior pits face posteroventrally rather than ventrally as in *Anakinetica*. These features indicate that substrate relationships would differ in some respect from *Anakinetica*.

Pilkena compressa sp. nov.

Fig. 6A-F

Name. From the Latin *compressus* (compressed).

Type material. Holotype NMV P3629 and paratypes NMV P3627-P3633, P134221 from the Gellibrand Marl (Janjukian, Upper Oligocene), 1.6 km west of Sherbrooke River, near Port Campbell, Victoria.

Additional locality. Jan Juc Formation (Janjukian): Bird Rock Cliffs, Torquay, Victoria.

Measurements. (In mm.)

Specimen	Total length	Dorsal valve length	Breadth	Depth
NMV P3629	27.2	22.4	20.1	9.9
NMV P3627	28.6	24.3	22.6	9.8
NMV P3631	27.3	23.0	20.4	10.3
NMV P3632	25.2	21.8	20.0	9.8
NMV P3628	20.8	18.2	14.9	7.2

Description. Outline ovate, shallowly biconvex, ventral valve carinate, dorsal valve sulcate. Symphytium flat with median ridge. Cardinal platform outline triangular with broad anterior base narrowing to posterior apex; central rounded area (presumed anterior surface of cardinal process) bordered laterally by socket ridges, posterolaterally by pits and posteriorly by posterior surface of cardinal process. Median septum short, thick, with blade-like ventral edge, without traces of connecting bands. Teeth triangular, base almost flush with edge of valve, walls not excessively thickened.

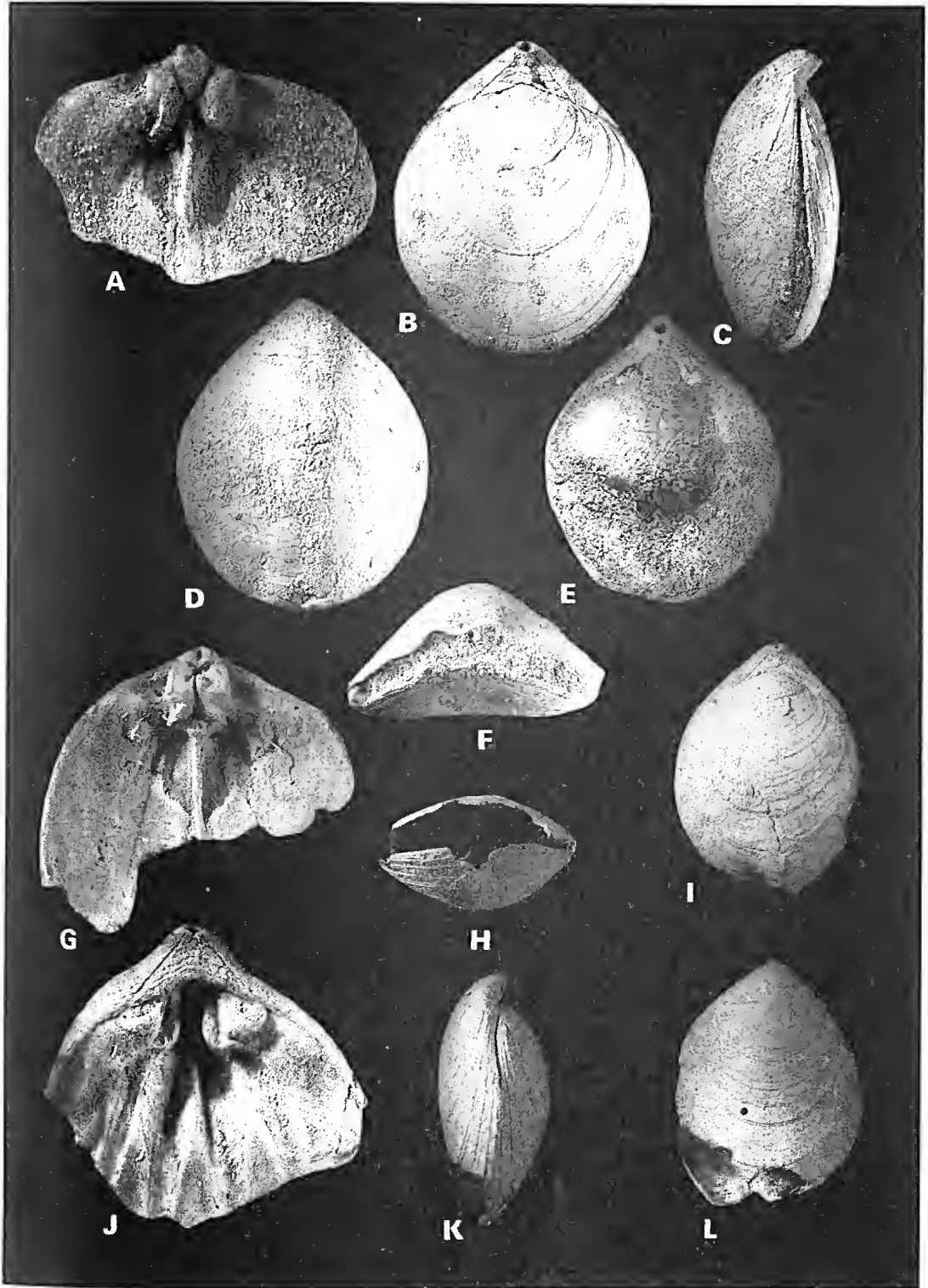
Aliquantula gen. nov.

Name. From Latin *aliquantulus* (small), in reference to the foramen.

Type species. *Waldheimia*(?) *insolita* Tate, 1880 from the Eocene of Australia.

Diagnosis. Weakly sulcate. Beak suberect, foramen small; beak ridges sharp; cardinal margin curved. Hinge platform with small posterior hinge trough; swollen crural bases fused or almost fused medially; socket ridges not projecting beyond umbo; cardinal process small, discrete. Loop without septal connecting bands.

Fig. 6. A-F, *Pilkena compressa* sp. nov. A, paratype NMV P3630, dorsal interior, $\times 2.5$. B-D, F, holotype NMV P3629, dorsal, lateral, ventral and anterior (ventral valve uppermost) views, $\times 1.8$. E, paratype NMV P3633, ventral interior, $\times 1.5$. G-L, *Aliquantula insolita* (Tate, 1880). G, NMV P134775, dorsal interior, $\times 2.3$. H, I, K, L, NMV P134774, anterior (ventral valve uppermost), dorsal, lateral and ventral views, $\times 1.3$. J, NMV P134776, ventral interior, $\times 2.3$.



Comments. The partial to total infilling of the hinge trough is one of the characteristic features of members of the Anakineticinae. *Magadinella* and young individuals of *Anakinetica* and *Parakinetica* show that reduction in size and/or total infilling of the hinge trough is the result of enlargement of the cardinal process (anterior surface) which fuses anteriorly with the crural bases. *Aliquantula* shows a different mode of infilling, with swollen crural bases which may be fused medially but which do not fuse with the cardinal process. As a result, a tiny posterior hinge trough is delimited. In characters of the cardinalia, *Aliquantula* closely resembles the Japanese genus *Nipponithyris*, but the latter differs in beak characters and in loop pattern.

Aliquantula insolita (Tate, 1880)

Fig. 6G-L

Waldheimia(?) *insolita* Tate 1880: 151-152 (partim.), pl. 9, fig. 6b.

Magellania insolita Tate 1899: 282 (partim.).

(?) *Stethothyris*(?) *insolita* Thomson 1927: 282.

Type material. Syntypes SAM T908A-E, G, H, from the Tortachilla Limestone (Eocene), Maslin Bay, Aldinga, South Australia.

Other horizons and localities. South Australia. Blanche Point Marl (Eocene): Maslin Bay, Aldinga. Victoria. Castle Cove Limestone (Lower Oligocene): Castle Cove (Wilks' locality No.5); mouth of Johanna River. Browns Creek Clay (Eocene): Browns Creek, Aire River district. Browns Creek Clay, greensand member (Eocene): Hamilton Creek, Aire River district. Material cited is housed in the Museum of Victoria.

Description. Length of figured specimen (Fig. 6 H-I, K-L) 28.8 mm, dorsal valve length, 25.4 mm, breadth 22.1 mm, depth 12.4 mm. Outline ovate, biconvex. Anterior commissure slightly sulcate. Hinge platform outline ovate; socket ridges incurved, not projecting beyond valve margin; crural bases fused with anterior halves of socket ridges; posterior hinge trough small, deep; cardinal process almost circular in outline, anterior surface slightly swollen. Septum short, blade-like, without loop attachments. Ventral valve interior with heavily thickened postero-lateral walls, beak cavity reduced to narrow tunnel. Hinge teeth irregular in outline, overlying heavy lateral thickenings in posterior region of valve immediately anterior to beak.

Comments. Of Tate's syntypes, specimen SAM T908A has previously been referred to *Aldingia furculifera* by Richardson (1973a).

ACKNOWLEDGEMENTS

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KYARRANUS MOORE (ANURA, LEPTODACTYLIDAE) FROM THE TERTIARY OF QUEENSLAND

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TYLER, M.J., 1991:06:30. *Kyarranus* Moore (Anura, Leptodactylidae) from the Tertiary of Queensland. *Proceedings of the Royal Society of Victoria* 103 (1): 47–51. ISSN 0035-9211.

The first fossil record of the leptodactylid frog *Kyarranus* Moore is from the Tertiary of northwestern Queensland. Sixteen specimens of the new species *K. borealis* have been recovered and described from a series of Oligo–Miocene sites far to the north of the geographic range of the three extant congeners. Ilial characters provide evidence to sustain the recognition of *Philoria* Parker as a distinct genus.

THE LEPTODACTYLID frog genus *Kyarranus* Moore, 1958 was erected to accommodate the species *K. sphagnicolus* Moore, 1958 from northeastern New South Wales, and *Philoria loveridgei* Parker (1940) from the adjacent portion of southeastern Queensland. A third species subsequently was referred to it, *K. kundagungan* Ingram & Corben, 1975.

Kyarranus is most closely related to the genuinely monotypic *Philoria* Spencer of Mt Baw Baw, Victoria. Each of the *Kyarranus* and *Philoria* species is restricted to localised montane habitats. The breeding biology is specialised. In both genera macrolecithal eggs are laid in moist situations out of water. Larval mouthparts are rudimentary and development is accomplished without feeding (Moore 1961, Littlejohn 1963, Anstis 1981).

Kyarranus has not been reported in the fossil record. However, a series of ilia clearly referable to this genus has been recovered recently from a series of Oligo–Miocene sites at Riversleigh Station in northwestern Queensland. In the present paper the specimens are described as a new species, and the geographic and palaeoclimatic significance of the discovery is discussed.

MATERIAL AND METHODS

The fossil material is deposited in the collections of the Queensland Museum, Brisbane (QM) and the South Australian Museum, Adelaide (SAM). Letters following the abbreviations are departmental identifications.

Comparative studies were based on osteological collections of the Department of Zoology, University of Adelaide. Osteological nomenclature follows Tyler (1976). Methods of measure-

ment and orientation of specimens follows the techniques described by Tyler (1989).

Details of sites, stratigraphy, etc. are provided by Archer et al. (1989).

SYSTEMATICS

Family LEPTODACTYLIDAE Werner, 1896
Subfamily LIMNODYNASTINAE Lynch, 1971

Genus *Kyarranus* Moore, 1958

The description of the ilial features of the genus by Tyler (1976) was based on *K. sphagnicolus* and *K. kundagungan* (reported there as "*Kyarranus* sp."). Since that date specimens of *K. loveridgei* have become available, and they do not differ conspicuously from the other species (Fig. 1). In all species the dorsal prominence and dorsal protuberance are particularly well-developed, and commonly project anteriorly as a spine. This feature is unique to *Kyarranus*.

Kyarranus borealis sp. nov.

Fig. 2

Holotype. QM F18167, an almost entire left ilium collected at RSO Site, Riversleigh Station, Queensland.

Description of holotype. Ilial shaft cylindrical and very slightly curved; almost entire. Very shallow grooves on medial surface at proximal and distal extremities.

Acetabular fossa very large, deep and with prominent rim bounding inferior half. Dorsal margin of acetabular fossa situated slightly superior to inferior margin of ilial shaft. Pre-acetabular zone evenly rounded and moderately



Fig. 1. Comparison of ilia of extant species of *Philoria* and *Kyarranus*. A, *Philoria frosti*; B, *Kyarranus kundagungan*; C, *K. loveridgei*; D, *K. sphagnicolus*. Scale bar = 5 mm.

developed. Ventral acetabular expansion (VAE) missing. Dorsal acetabular expansion (DAE) narrow and incomplete. Dorsal prominence well-developed and conspicuous. Dorsal protuberance projecting laterally and extremely conspicuous. Anterior margin of dorsal prominence extends to position located anterior to anterior margin of acetabulum.

Length of ilium 16.1 mm; DAE/VAE cannot be estimated with any degree of confidence.

Paratypes. There are 15 paratypes: Gag Site QM 18160, 18166, SAM P31237; Last Minute Site QM F18163; Neville's Garden Site QM F18169–70, R.S.O. Site QM F18161, 18165; Camel Sputum Site QM F18162, 18168, 18171,

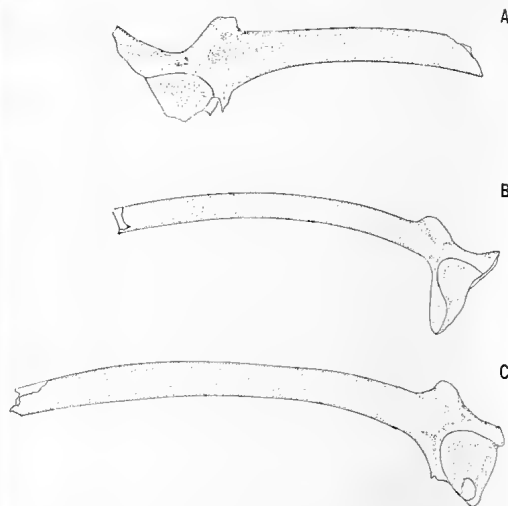


Fig. 2. Ilia of *Kyarranus borealis* sp. nov. A, QM F18169 (paratype); B, SAM P31238 (paratype); C, QM F18167 (holotype).

SAM P31238; Upper Site SAM P31239; Outsite Site QM F18172; Wayne's Wok Site QM F18164.

Variation. Fourteen of the 15 paratypes have an incomplete shaft. The complete specimen (SAM P31238) measures 8.7 mm compared with 16.1 mm for the holotype. No significance is attributed to this difference beyond ontogenetic; comparable variation in size was noted in *Lechriodus intergerivus* at Riversleigh Station (Tyler 1989) and the projected sizes of many of the incomplete ilia approximate the holotype. The proximal portions of each of the ilia, although commonly lacking entire dorsal or ventral acetabular expansions, conform to the shape of the holotype.

Comparison with other species. It is evident that *K. borealis* may have been a slightly larger species than any of the extant congeners. As determined by plotting the regression line of ilial length upon snout to vent length of extant species (Fig. 3), the holotype of *K. borealis* would have had a snout to vent length of 37.9 ± 0.67 mm. This figure compares with upper limits of 31 mm for *K. loveridgei*, 30 mm for *K. kundagungan* and 37 mm for *K. sphagnicolus*.

Etymology. The adoption of *borealis* (L.) or "northern" refers to the far northern position of the type locality compared with the geographic distributions of extant species.

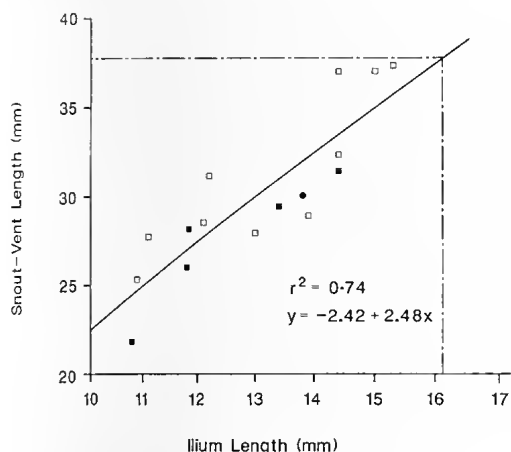


Fig. 3. Length of ilia of *Kyarranus* species plotted against snout to vent length. Assumed snout to vent length of largest specimen of fossil species indicated by broken lines, t -value for slope 6.365, $p < 0.001$. For $x = 16.1$, $y = 37.9$ (95% confidence limits = 36.8–38.2). Closed squares = *K. loveridgei*; open squares = *K. sphagnicolus*; closed circle = *K. kundagungan*.

DISCUSSION

Discovery of *Kyarranus* in the Tertiary of northern Queensland is significant in its contribution to an understanding of the origin and dispersal of Australian frogs and the palaeoenvironmental implications. Extant *Kyarranus* are confined to three isolated montane areas which are variously forested, and where there is a carpet of low growing vegetation and decomposing material within which the frogs live and deposit spawn.

The three extant *Kyarranus* species are allopatric and clustered around the eastern extremity of the Queensland–New South Wales border (Fig. 4). The evident close phylogenetic relationship to *Phyllorhina* that has caused the status of *Kyarranus* to be questioned indicates that a shared ancestral stock once extended through New South Wales and eastern Victoria.

The presence of *K. borealis* in the Tertiary of northwestern Queensland indicates a much more widespread geographic distribution than has been appreciated, and emphasises the relict nature of the extant populations. Extinction in the northwest and intermediate areas can be attributed to the first onset of aridity. However, the existence at the Riversleigh sites raises the question of why this genus did not extend its range farther north into New Guinea when opportunities arose.

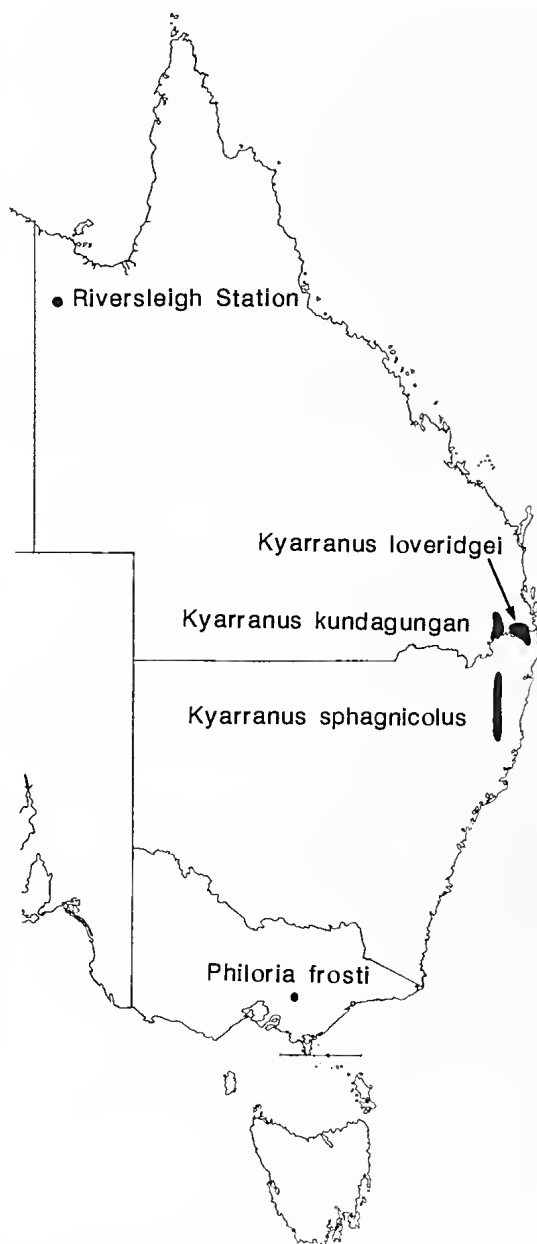


Fig. 4. Geographic distribution of species of *Kyarranus* and *Phyllorhina*. The extent of *K. sphagnicolus* so far south is based on locality records of Webb (1989).

A partial parallel is the distribution of *Lechriodactylus* Boulenger which is abundant at Riversleigh sites but exhibits a similar gap to the northern limit of the (single) extant species (Tyler 1989, Tyler et al. 1990). However, *Lechriodactylus* has three extant species in New Guinea.

Conceivably *Kyarranus* does occur in the New Guinea highlands but has yet to be found there. This proposition is plausible when it is noted that the leptodactylid genus *Mixophyes* Günther, with five members well-known from the rainforests of eastern Australia, has only recently been reported from New Guinea (Donnellan et al. 1990). If such large and conspicuous frogs escaped attention, the absence of *Kyarranus* in New Guinea may be more apparent than real.

The only area in Australia where the suite of genera reported from Riversleigh (*Lechriodus*, *Limnodynastes* Fitzinger, *Crinia* Girard, *Litoria* Tschudi and *Kyarranus*) coexist today is along the Queensland–New South Wales border. Three of the genera (*Kyarranus*, *Lechriodus* and *Limnodynastes*) share the habit of depositing ova in a foam nest. The last two (and *Megistolotis*) create the nest in an identical fashion (Tyler & Davies 1979), but the method in *Kyarranus* (and *Philoria*) has not been observed. Given the complexity of that behavioural activity, concepts of parsimony dictate that the habit evolved in a common ancestor. Elucidation of the Riversleigh frog fauna will clearly lead to an understanding of Oligo–Miocene environments there.

Cogger, Cameron & Cogger (1983) referred *Kyarranus* to the synonymy of the monotypic genus *Philoria* Spencer of Mt Baw Baw in Victoria but did not provide information to substantiate that decision. Accordingly, the synonymy was not accepted by Frost (1985). *Kyarranus* is smaller than *Philoria*, and lacks the hypertrophied dermal glands of that genus. The genera also differ in the arrangement of several skull bones, as pointed out by Lynch (1971). The ilium of *Philoria* differs from that of *Kyarranus* in having a lower dorsal, acetabular expansion, a much less pronounced dorsal prominence and dorsal protuberance, and a reduced pre-acetabular zone (Fig. 1). Given the inherent conservatism of the ilium, the distinctions listed above support the recognition of *Kyarranus* as distinct from *Philoria*.

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I thank Professor Michael Archer, Mr Henk Godthelp and Dr Suzanne Hand of the University of New South Wales for their continued aid and support in the preparation and isolation of material.

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Reed and Miss Leanne Seller provided invaluable support, whilst Ms Rachel Norris assisted in statistical analysis. Specimens of extant species were provided by Mr J. de Bavay (University of New England), Dr G. Ingram (Queensland Museum) and Mr Ross Sadlier (Australian Museum). Research facilities were provided by the University of Adelaide, and the manuscript was typed by Mrs L. Lucas.

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OBITUARY

DR R. R. GARRAN



DR RICHARD GARRAN, a life member of the Royal Society of Victoria, died on 8 April 1991, aged 88 years.

Dick, a son of Sir Robert Garran, took his first degree in science at Trinity College, Melbourne University where, apart from his academic pursuits, he distinguished himself by his rowing

prowess. From Melbourne he crossed to Imperial College, London to carry out his postgraduate research. From there, he joined what became the Alkali Division of ICI at Winnington, England, in a select group who were regarded then as the scientific aristocrats of the company.

In the early 1930s, Dick was involved in plans to establish alkali manufacture in Australia, and just before World War 2 came to Osborne in South Australia to take charge of what became a successful operation. There he earned quite a reputation for his hard work and his ability to work remarkably long hours without intermission. He spent his last two or three years with ICI at head office, Melbourne, in charge of personnel.

Dick joined the Royal Society of Victoria in 1954, becoming a member of Council in 1957, and was President in 1961–62. From 1969 to 1983 he acted as Honorary Executive Officer for the Society. In recognition of his services to the Society he was made a Life Member in 1983.

At first encounter, Dick seemed a rather quiet, reserved man. On better acquaintance, he proved to be a very warm-hearted person, a cultured, gentle man in the very highest sense, with a delightful dry sense of humour. He will be missed very much by his friends.

J. D. M.

STUDIES ON WESTERN AUSTRALIAN PERMIAN BRACHIOPODS 10. FAUNAS FROM THE WOORAMEL GROUP, CARNARVON BASIN

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ARCHBOLD, N. W., 1991:12:31. Studies on Western Australian Permian brachiopods 10. Faunas from the Wooramel Group, Carnarvon Basin. *Proceedings of the Royal Society of Victoria* 103 (2): 55-66. ISSN 0035-9211.

The brachiopod faunas from the One Gum and Billidee Formations of the Wooramel Group are reviewed and described. The new species *Neochonetes (Sommeriella) loockingi* is described and the *Strophalosia jimbaensis* zone is proposed for the faunas described herein. The age of the *Strophalosia jimbaensis* zone is discussed, with an Aktastinian (Early Artinskian) age being preferred.

FOR MANY years there has been considerable debate about the stratigraphical and age significance of the Early Permian marine faunas from the Wooramel Group of the Carnarvon Basin. This study investigates the relatively small collections of variably preserved specimens from the dominantly arenaceous sections of the Wooramel Group sequence. A larger fauna from the Jimba Jimba Calcarenite Member will be documented elsewhere, in view of some confusion over the recognition of this unit in the field (cf. Condon 1967, Hocking et al. 1987).

STRATIGRAPHY

The Permian stratigraphy of the Carnarvon Basin was extensively described by Condon (1967) on the basis of mapping by Bureau of Mineral Resources field parties, and was reviewed and revised by Hocking et al. (1987) on the basis of mapping by Geological Survey of Western Australia field parties. Only the pertinent stratigraphy concerning the Wooramel Group is summarised herein.

The Wooramel Group was defined by Konecki et al. (1958: 28) as the predominantly arenaceous sequence, with few marine fossils, above the surface of the disconformity on top of the Callytharra Formation and conformably below the Byro Group. They divided the Group into three formations (the Nunnery Sandstone, One Gum Formation and Keogh Formation in ascending order) in the type locality region on the Wooramel River, Byro Sub-Basin. The Wooramel Group interval of sediments had previously been recognised by such workers as Condit (1935), Condit et al. (1936), Raggatt (1936), Teichert (1952) and Condon (1954). McWhae et al. (1958) had access to the manu-

script of Konecki et al. (1958) and were the first to cite the names of the formations proposed by Konecki et al.

Other formations in the Wooramel Group were named or described by Condon (1954, 1962a, 1962b, 1965) and in McWhae et al. (1958). Substantial simplification and revisions of the terminology of the Wooramel Group were proposed by van de Graaff et al. (1977) and Hocking et al. (1980). The collections described in the present study come from the One Gum Formation, Byro Sub-Basin (*sensu* Konecki et al. 1958, also Dickins 1956) and the Billidee Formation of the Merlinleigh Sub-Basin (*sensu* Hocking et al. 1987). For convenience, these two stratigraphical names are used in this study.

PREVIOUS FAUNAL STUDIES

Most faunal studies involving the Wooramel Group assemblages have been based on field observations or unpublished palaeontological reports (e.g. see Condon 1962a, 1967, Dickins 1956, Cockbain 1979). On the basis of material observed and collected by Bureau of Mineral Resources field parties during the 1950s, Dickins (1963) was able to demonstrate that the bulk of the Wooramel Group was characterised by "rather unsatisfactory" material that appeared to be "closer to the older Fossil Cliff/Nura Nura assemblage than to the younger fauna of the Byro Group" (Dickins 1963: 14). This was to characterise Stage C marine faunas of the Western Australian Permian sequences which were "marked by the absence rather than the presence of a marine fauna" (Dickins 1963: 20).

Dickins (1963: 14) also drew attention to the small bivalve and brachiopod fauna in the top-

most beds of the Wooramel Group which is identical with the fauna found in the immediately overlying Byro Group, reflecting "the deepening of the basin and the initial development of more definite off-shore marine conditions in those places". This fauna, found in the top of the Keogh and Billidee Formations, was included in Stage D by Dickins (1963). The occurrence of the ammonoids *Neocrimites* sp. and *Bamyaniceras* sp. in beds high in the Billidee Formation (Cockbain 1980) also links this fauna with the lowest fauna of the Byro Group, generally regarded as being early Baigendzhinian in age.

While there is little disagreement as to the age of the uppermost Wooramel Group faunas, this is not the case for the bulk of the Wooramel Group. Dickins (1963) considered that the close relationship of his Stage C assemblages with those of his Stage B assemblages indicated an age for Stage C of Early Artinskian (Aktastinian). He considered Stage C to be immediately younger than the Sterlitamakian fauna of the underlying Callytharra Formation with, by implication, the disconformity between the two stratigraphical units representing a very minor interval of time.

However, the discovery of a specimen of the ammonoid *Pseudoschistoceras* from beds near the top of the Cordalia Sandstone (a lateral equivalent of the Nunnery Sandstone) resulted in Cockbain (1980) considering the entire Wooramel Group to be of early Baigendzhinian age. *Pseudoschistoceras* is generally considered to indicate a Baigendzhinian age (Glenister et al. 1983) but is only known from three described localities and is listed from the Kungurian by Bogoslovskaya (1988), indicating that its full stratigraphical range may not be fully understood. Runnegar (1969) and Waterhouse (1970) regarded the recognition of Stage C as unwarranted and so merged it with Stage B. As a result Cockbain (1980: 104) considered that Stage B had a "fairly long time range and occurs at a number of shelly horizons, often of limited extent, and hence cannot be used for detailed biostratigraphical correlation".

AGE OF WOORAMEL GROUP

The fossils figured and described herein include the following:

?*Streptorhynchus* sp.

Perrinorthotetes sp.

Neochonetes (*Sommeriella*) *hockingi* sp. nov.

Strophalosia jimbaensis Archbold, 1986

Aulosteges sp.

Fusispirifer sp.

Neospirifer sp.

?*Cleiothyridina* sp.

?*Aviculopecten* sp.

While the preservation of specimens as natural ferruginous casts and internal and external moulds is of variable quality, the overall affinity of the fauna is closer to that of the Callytharra Formation than to that of the overlying fauna of the Madeline/Coyrie Formation. Nevertheless the Wooramel Group species are distinctive, and of particular importance are species of *Neochonetes* (*Sommeriella*) and *Strophalosia*. Chonetid brachiopods evolved rapidly during the Permian in Western Australia (e.g. see Archbold 1981) and are invaluable for correlation, while *Strophalosia* species are also important for biostratigraphy (e.g. see Clarke 1990).

A formal zone is proposed herein for Wooramel Group faunas, namely the *Strophalosia jimbaensis* zone, based on a species that is found in both the One Gum and Billidee Formations. The species is also present in the Jimba Jimba Calcarenite where the distinctive species *Globiella flexnosa* (Waterhouse) is also found (Archbold 1983). The Jimba Jimba fauna, currently being investigated by me, appears to be related to that of the Callytharra Formation but is distinct at the species level, adding support to the biostratigraphical recognition of Stage C of Dickins (1963).

In view of the relatively close relationship of many of the Wooramel Group species to those from the Callytharra Formation (see comparisons below), I agree with Dickins (1963) that the disconformity between the two units does not represent a major break in time (perhaps just the late Sterlitamakian). As a result, notwithstanding the significance of the occurrence of the ammonoid *Pseudoschistoceras* sp., I prefer an Aktastinian age assignment for the Wooramel Group. Comparison of a few species of the fauna with forms from Sterlitamakian or Aktastinian horizons elsewhere also strengthens the proposed Aktastinian age.

COLLECTIONS AND LOCALITIES

All specimens are registered with the Geological Survey of Western Australia (GSWA F), Perth or with the Commonwealth Palaeontological Collections (CPC) of the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Specimens were found at the following localities:

Geological Survey of Western Australia locality 94217, from a solitary peak west of Mt Sandiman–Moogooree Road about 12 km north of Mt Sandiman Homestead, Kennedy Range 1:250,000 sheet. Photo reference, Kennedy Range 1968: Run 3, Photo 214, Point 547. From midway up hill where two coquina bands outcrop. Lower band with *Neochonetes* (*Sommeriella*) and upper (2 m higher) with *Strophalosia*. Billidee Formation.

Bureau of Mineral Resources locality WB 9, 1.25 miles (2 km) on a bearing of 285° from Keogh Hill. Base of One Gum Formation.

Bureau of Mineral Resources locality WB 69, 2.24 miles (3.5 km) on a bearing of 258° from Keogh Hill. Base of One Gum Formation.

Bureau of Mineral Resources locality 7864, 0427, Glenburgh Run 13A, Photo 5009, 2.4 km on a bearing of 276° from Keogh Hill. Base of One Gum Formation.

SYSTEMATIC PALAEOONTOLOGY

Phylum BRACHIOPODA

Order STROPHOMENIDA Öpik, 1934

Suborder ORTHOTETIDINA Waagen, 1884

Superfamily ORTHOTETACEA Waagen, 1884

Family STREPTORHYNCHIDAE Stehli, 1954

Genus *Streptorhynchus* King, 1850

Type species. Terebratulites pelargonatus Schlotheim, 1816.

?*Streptorhynchus* sp.

Fig. 1C

Comments. A single specimen (CPC 24502) of a ferruginous cast of a dorsal valve exterior (specimen 24 mm wide, 26 mm long) may represent the occurrence of *Streptorhynchus* or a related genus in the basal One Gum Formation assemblage (locality BMR 7864, 0427). The specimen

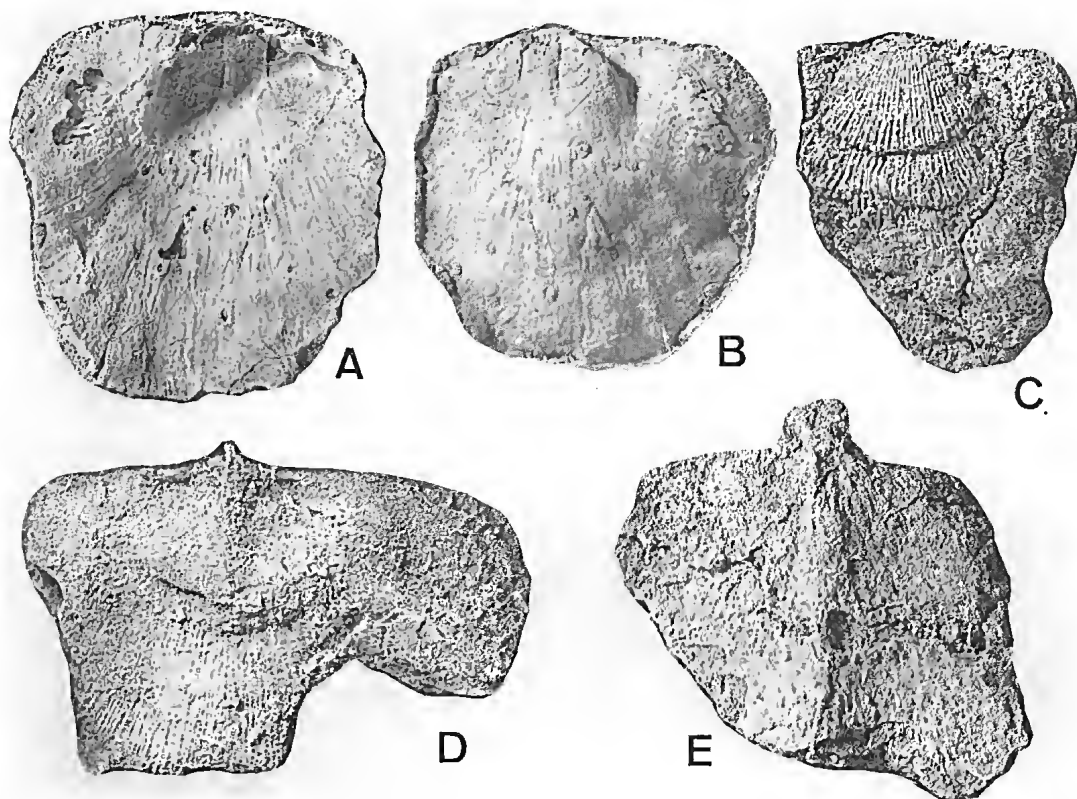


Fig. 1. A, B, *Permorthotetes* sp. A, B, CPC 24503, latex cast of incomplete dorsal valve internal mould and the internal mould, $\times 1.4$, $\times 1.2$. D, CPC 24504, natural cast of ventral valve exterior, $\times 1$. C, ?*Streptorhynchus* sp., CPC 24502, natural cast of incomplete dorsal valve, $\times 1.5$. E, *Aulosteges* sp., CPC 24505, natural cast of dorsal valve exterior, $\times 1$.

possesses distinct concentric growth interruptions as in *Arctitreta plicatilis* (Hosking) as described by Thomas (1958), but indicates a larger species than the *Callytharra* species. Costellae number 8 to 12 per 5 mm and increase predominantly by intercalation although rare bifurcation does occur. Costellae are gently rounded and broaden anteriorly, and hence are not flattened as in *Arctitreta plicatilis* but rather resemble those of *Streptorhynchus crassimurus* Thomas, 1958 from the late Baigendzhinian Noonkanbah Formation, Canning Basin.

Family ORTHOTETIDAE Waagen, 1884
Subfamily ORTHOTETINAE Waagen, 1884

Genus *Permorthotetes* Thomas, 1958

Type species. *Permorthotetes callytharrens* Thomas, 1958.

Permorthotetes sp.

Fig. 1A, B, D

Permorthotetes sp.—Thomas 1958: 107.—Condon 1962a: 11.—Condon 1967: 102.

Orthotetacea nov. gen.—Konecki et al. 1958: 33.

Material. One incomplete mould of a dorsal valve (CPC 24503) from locality BMR 7864, 0427, width 38.5+ mm, length 42+ mm; and one natural cast of a ventral valve exterior (CPC 24504) from locality BMR WB 9, width 67+ mm, length 42 mm.

Comments. Two specimens are consistent with the identification of *Permorthotetes* from the basal One Gum Formation. The dorsal valve internal mould reveals an uneven convex profile and a low median ridge bisecting the muscle field. The cardinal process is unknown. The ventral valve external ferruginous cast is large, wrinkled, irregularly gently convex posteriorly and flat anteriorly. Costellae are fine (about 7 to 8 per 5 mm at 30 to 40 mm from umbo) and increase by intercalation. Intercostal troughs are

wider than costellae. A comparison with *Permorthotetes callytharrens* Thomas, 1958 is suggested but better material is required for detailed comparisons.

Order CHONETIDA Nalivkin, 1979
Suborder CHONETIDINA Muir-Wood, 1955
Superfamily CHONETACEA Bronn, 1862
Family RUGOSCHONETIDAE
Muir-Wood, 1962
Subfamily RUGOSCHONETINAE
Muir-Wood, 1962

Genus *Neochonetes* Muir-Wood, 1962
Subgenus *Neochonetes* (Sommeriella)
Archbold, 1982

Type species. *Chonetes prattii* Davidson, 1859.

Comments. The subgeneric name *Sommeriella* Archbold, 1981 was replaced by the name *Sommeriella* by Archbold, 1982. The recognition of subgenera within the large and widely understood genus *Neochonetes* was discussed by Archbold (1981).

Neochonetes hockingi sp. nov.

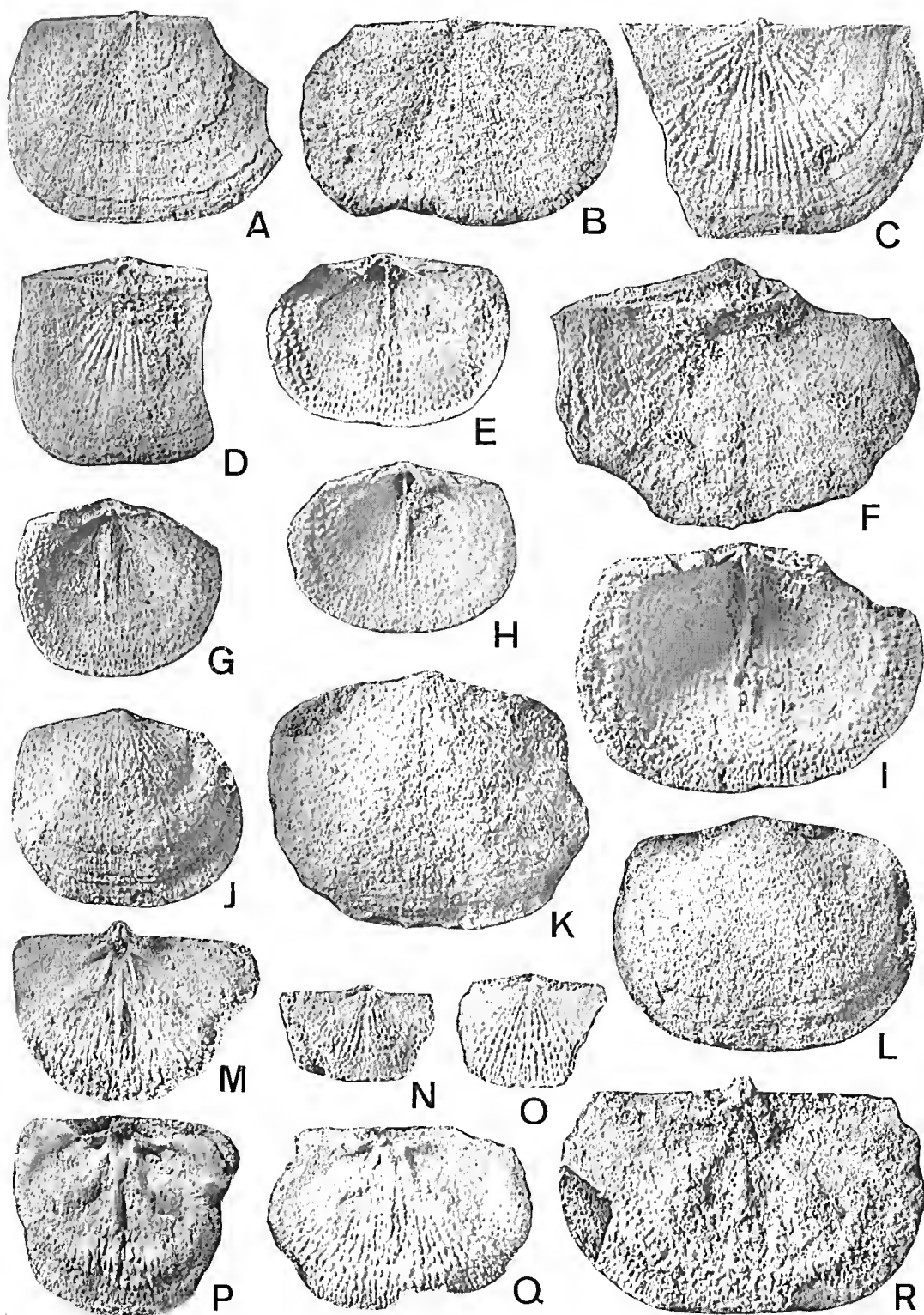
Fig 2A–R

Etymology. Named for geologist Roger M. Hocking, discoverer of the chonetid band which yielded the species.

Holotype. GSWA F11247, a natural ferruginous cast of a ventral valve exterior showing the external ornament, from GSWA locality 94217, Billidee Formation, collected by Dr S. K. Skwarko, Geological Survey of Western Australia.

Paratypes. GSWA F43818–F43820, two natural casts of dorsal valve exteriors and one external mould of a dorsal valve; GSWA F43821, F43822, two natural casts of shells; GSWA F43823–F43826, four natural casts of ventral valve interiors; GSWA F43827, F43828, two natural casts of ventral valve exteriors; and GSWA F43829–F43834, five natural casts of dorsal valve interiors and one natural internal mould of a

Fig. 2. *Neochonetes (Sommeriella) hockingi* sp. nov. A, GSWA F43818, natural cast of dorsal valve exterior, $\times 3.5$. B, GSWA F43819, latex cast of dorsal valve exterior, $\times 3.5$. C, GSWA F43820, natural cast of dorsal valve exterior, $\times 3.5$. D, GSWA F43821, natural cast of shell in dorsal view, $\times 3.5$. E, GSWA F43823, natural cast of ventral valve interior, $\times 3.5$. F, GSWA F43822, natural cast of shell in dorsal view, $\times 3.5$. G, GSWA F43824, natural cast of ventral valve interior, $\times 3.5$. H, GSWA F43825, natural cast ventral valve interior, $\times 3.5$. I, GSWA F43826, natural cast of ventral valve interior, $\times 3.5$. J, GSWA F11247, holotype, natural cast of ventral valve exterior, $\times 3.5$. K, GSWA F43827, natural cast of ventral valve exterior, $\times 3.5$. L, GSWA F43828, natural cast of worn ventral valve exterior, $\times 3.5$. M, GSWA F43829, natural cast of dorsal valve interior, $\times 3.5$. N, GSWA F43830, natural cast of juvenile dorsal valve interior, $\times 3.5$. O, GSWA F43831, natural cast of juvenile dorsal valve interior, $\times 3.5$. P, GSWA F43832, latex cast of dorsal valve internal mould, $\times 3.5$. Q, GSWA F43833, natural cast of dorsal valve interior, $\times 3.5$. R, GSWA F43834, natural cast of dorsal valve interior, $\times 3.5$.



dorsal valve; same locality and collector as holotype.

Size ranges. Maximum width 5.7–14.9 mm; hinge width 5.5–14.2 mm; ventral length 6.5–10.6 mm; dorsal length 4.3–9.3 mm.

Diagnosis. Small *Neochonetes* (*Sommeriella*). Ventral sulcus weakly developed; dorsal fold low but distinct. External ornament of fine capillae, on average numbering 3 per mm at 6 mm from umbones.

Description. Length of shell just over two-thirds of maximum width. Maximum width just anterior of shell mid-length; hinge width less than maximum width. Ventral valve evenly convex. Sulcus low, broadening anteriorly, arising close to umbo. Dorsal valve gently concave with low median fold often poorly developed. Interareas low, chilidium and pseudodeltidium poorly known. Ornament of capillae increasing by bifurcation and intercalation. Growth lines fine, more pronounced anteriorly.

Casts of worn ventral valves show external ornament poorly; those of worn dorsal valves show progressive absence of growth lines and presence of fine pseudocapillate ornament (5–6 per mm at 6 mm from umbo) reflecting internal subsurface shell structure. Ventral hinge spines poorly known, appear to project at 40° to 45°.

Ventral interior with distinct median septum, over half valve length at maturity, arising under ventral umbo. Parallel vascular trunks usually distinct adjacent to septum. Adductor scars indistinct; diductors large, prominent, gently striated. Remainder of valve floor papillose. Teeth small, sharp.

Cardinal process internally bilobate, externally poorly known. Dorsal median septum distinct, up to 0.6 times valve length. Ontogeny of dorsal septum reveals absence in juveniles, presence well to the anterior of alveolus in submaturity but fused with lateral septa and anterior of alveolus at maturity. Sockets distinct

with pronounced inner socket ridges. Brachial ridges raised and papillose at maturity. Radiating rows of papillae in anterior of dorsal valve.

Discussion. *Neochonetes* (*Sommeriella*) *hockingi* is distinguished from most other Western Australian representatives of the subgenus by its distinctive small size and low ventral sulcus. *N. (S.) robustus* Archbold, 1981 from the early Baigendzhinian Madeline Formation, Carnarvon Basin, is a slightly larger species with a distinctive rounded outline and is more concavo-convex than *N. (S.) hockingi*. The sulcus of *N. (S.) robustus* is virtually absent. The new species shares features with *N. (S.) arabicus* (Hudson & Sudbury, 1959) from the Sterlitamakian to Aktastinian or younger Lusaba Limestone of Oman, an even smaller species with similar dorsal exterior and interior to those of *N. (S.) hockingi*. The Oman species is the smallest representative of *Neochonetes* (*Sommeriella*) known at present (Archbold & Burrett 1990).

Order PRODUCTIDA Sarycheva & Sokolskaya, 1959

Suborder STROPHALOSIIDINA Waterhouse, 1975

Superfamily STROPHALOSIACEA Schuchert, 1913

Family STROPHALOSIIDAE Schuchert, 1913
Subfamily STROPHALOSIINAE Schuchert, 1913

Genus *Strophalosia* King, 1844

Type species. *Strophalosia gerardi* King, 1846.

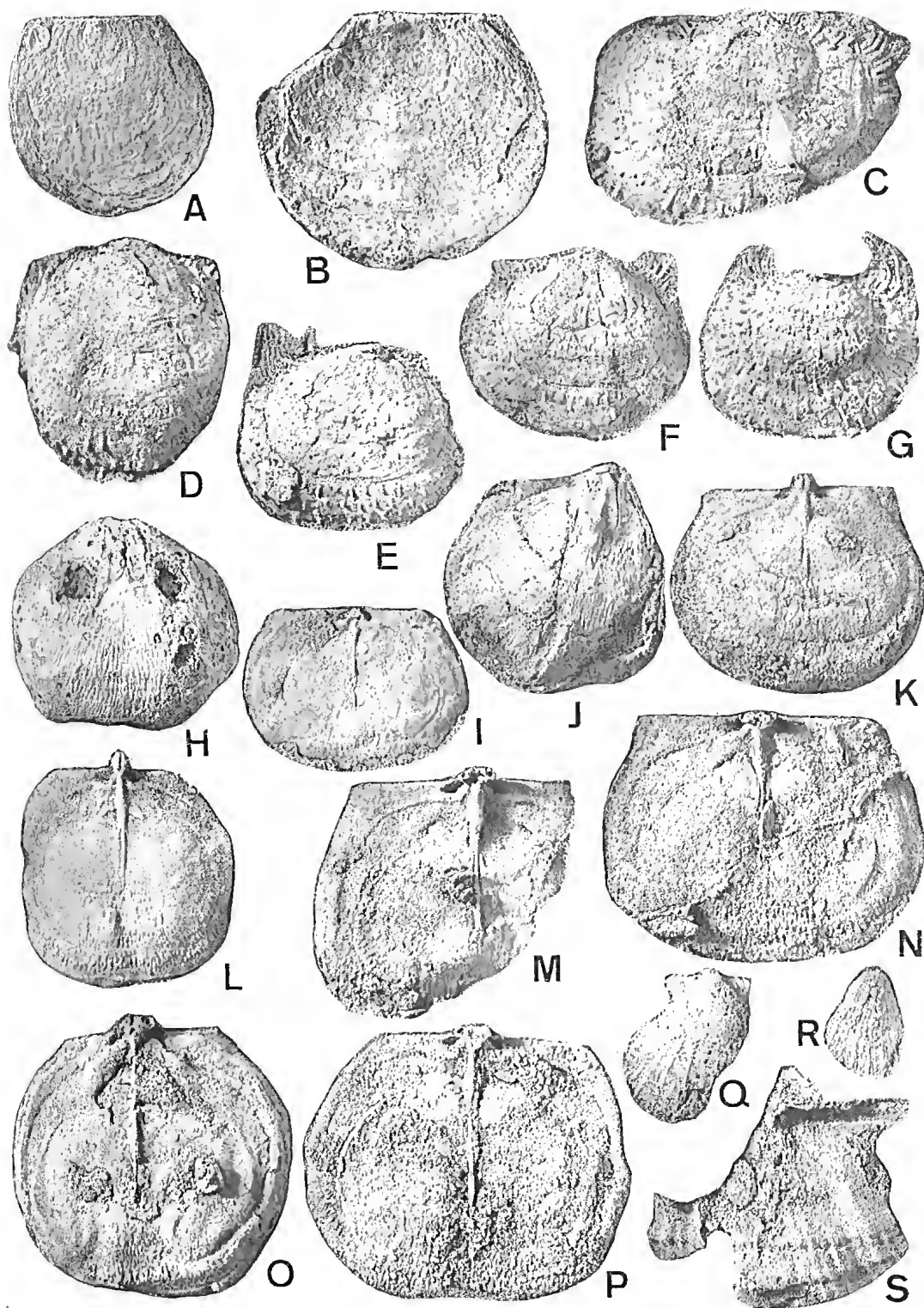
Strophalosia jimbaensis Archbold, 1986

Fig. 3A–P

Strophalosia nov. sp.—Konecki et al. 1958: 33.

Strophalosia sp.—Condon 1963a: 11.—Condon 1967: 114.—McGann 1976: 47.

Fig. 3. A–P, Strophalosia jimbaensis Archbold. A, GSWA F43835, natural cast of dorsal exterior, $\times 1.3$. B, GSWA F43836, natural cast of dorsal valve exterior, $\times 1.3$. C, GSWA F43837, latex cast of ventral valve external mould, $\times 1.3$. D, GSWA F43838, latex cast of ventral valve external mould, $\times 1.3$. E, GSWA F43839, latex cast of ventral valve external mould, $\times 1.3$. F, GSWA F43840, latex cast of ventral valve external mould, $\times 1.3$. G, GSWA F43841, latex cast of ventral valve external mould, $\times 1.3$. H, GSWA F43842, internal mould of ventral valve, $\times 1.3$. I, GSWA F43844, latex cast of dorsal valve internal mould, $\times 1.3$. J, GSWA F43843, latex mould from natural cast of dorsal valve interior, $\times 1.3$. K, GSWA F43845, latex cast of dorsal valve internal mould, $\times 1.3$. L, GSWA F43846, latex cast of dorsal valve internal mould, $\times 1.3$. M, GSWA F43847, latex cast of dorsal valve internal mould, $\times 1.3$. N, GSWA F43848, latex cast of dorsal valve internal mould, $\times 1.3$. O, GSWA F43849, latex cast of dorsal valve internal mould, $\times 1.3$. P, GSWA F43850, latex cast of dorsal valve internal mould, $\times 1.3$. Q, R?, *Aviculopecten* sp., GSWA F43852, F43853, two small specimens, both incomplete, $\times 1$. S, *Fusispirifer* sp., GSWA F43851, incomplete internal mould of ventral valve, $\times 1$.



Strophalosia jimbaensis Archbold 1986: 102–104, fig. 2A–G.

Strophalosia sp. cf. *S. jimbaensis*.—Archbold 1986: 104, fig. 2H–O.

Material. GSWA F43835–43850, two natural ferruginous casts of dorsal valve exteriors, five external moulds of ventral valves, one internal mould of a ventral valve, one natural cast of a ventral valve interior and seven internal moulds of dorsal valves, all from GSWA locality 94217, Billidee Formation, collected by Dr S. K. Skwarko, Geological Survey of Western Australia.

Size ranges. Maximum width 25.4–40.2 mm; hinge width 19.2–28.2 mm; ventral length 20.6–29.4 mm; dorsal length 19.6–32.6 mm.

Diagnosis. Medium to large sized *Strophalosia* with moderately convex ventral valve and concave dorsal valve. Dorsal valve with well defined dimples, growth lamellae and radial capillae, no spines. Ventral valve with hinge spines, two rows on ears, numerous scattered suberect body spines and a shallow median sulcus or flattening.

Comments. Dickins (in Konecki et al. 1958: 33) was the first to recognise "*Strophalosia* nov. sp., resembling a species from the Callytharra Formation" in the basal One Gum Formation assemblage. Eight specimens from the assemblage were figured by Archbold (1986, fig. 2H–O) who compared them with the Jimba Jimba Calcarenite species *Strophalosia jimbaensis*. Different styles of preservation between the type specimens of *S. jimbaensis* and the One Gum specimens prevented unequivocal assignment of the latter to *S. jimbaensis*.

The well preserved new suite of specimens from the Billidee Formation serves to unite the two collections discussed above and provides additional information on details of the ventral exterior spines and the dorsal interior and cardinal process. Spines on the ventral ears are in two rows and curve back towards the umbo; they are in excess of 8.5 mm in length. Body spines are in rough concentric rows and project laterally and anteriorly near the exterior perimeter of the ventral valve. The dorsal interior possesses a thin median septum about half the valve length at submaturity, but at maturity a thickened median septum is some two-thirds the valve length. Large brachial ridges become prominent at full maturity. The cardinal process is relatively small, bilobed internally and spike-like at submaturity when it projects posteriorly beyond the hinge line of the dorsal valve. At

maturity, the cardinal process is broader and more massive, approaches a quadrilobed state internally and projects internally in the plane of the dorsal interarea.

Several other species of *Strophalosia* have been described since the erection of *S. jimbaensis* by Archbold (1986). *Strophalosia perfecta* Waterhouse & Rao (1989) from the Early Permian of the Bap Formation, Rajasthan is a much smaller species than *S. jimbaensis*, suggesting comparison with the Western Australian Sterlitamakian species *S. irwinensis* Coleman (see Archbold 1986). *S. concentrica* Clarke, 1990 from the Early Permian of Tasmania is a distinct small to medium sized globose species that does not warrant close comparison with *S. jimbaensis*. *S. ?vollosovitschi* (Fredericks, 1931) as recorded by Abramov & Grigor'eva (1988: 104, pl. 1, figs 23–25, pl. 2, figs 1, 2, 7) from Verkhoyan'ya, northeast Siberia is a large species apparently lacking distinct dorsal external dimples.

Strophalosia is a characteristic genus of the Early Permian (Asselian–Sakmarian) of Australia (Archbold 1986, Clarke 1990) although ranging younger in Western Australia with the species *S. jimbaensis*. The genus is unknown in the well known Baigendzhinian faunas of the Carnarvon and Canning Basins, although a very rare species (2 specimens?) is known from the early Baigendzhinian fauna of the Mingenew Formation of the Perth Basin (Archbold 1988). The Mingenew species possesses distinctive smaller dorsal exterior dimples than those of *S. jimbaensis*.

Superfamily AULOSTEGACEA Muir-Wood & Cooper, 1960

Family AULOSTEGIDAE Muir-Wood & Cooper, 1960

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

Genus *Aulosteges* von Helmersen, 1847

Type species. *Orthis wangenheimi* de Verneuil, 1845 (= *Aulosteges variabilis* von Helmersen, 1847).

Aulosteges sp.

Fig. 1E

Comments. A single natural cast of the exterior of a dorsal valve (CPC 24505) from BMR locality WB 9, basal One Gum Formation, indicates the presence of *Aulosteges* s.l. in the assemblage, on the basis of its distinct, low dorsal median

fold. The specimen shows distinct dimples and a few spine bases but is inadequate for detailed comparison with other Western Australian species described by Coleman (1957).

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily SPIRIFERACEA King, 1846

Family SPIRIFERIDAE King, 1846

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Genus *Fusispirifer* Waterhouse, 1966

Type species. *Spirifer nitiensis* Diener, 1897.

Comments. *Fusispirifer* was reviewed by Archbold & Thomas (1987) who discussed the subfamilial placing of the genus and its palaeogeographical distribution. An additional species of *Fusispirifer* from the Western Australian Permian was described by Archbold & Skwarko (1988).

Fusispirifer sp.

Fig. 3S, 4A–G, L.

Material. CPC 19894–19897, three ventral valve internal moulds and one external mould of a ventral valve from BMR locality WB 69, basal One Gum Formation. CPC 24506–24509, two natural casts of juvenile ventral valve interiors and two incomplete external moulds of ventral valves from BMR locality 7864 0427, basal One Gum Formation. GSWA F43851 (formerly F11060/1), incomplete internal mould of a ventral valve from GSWA locality 94217, Billidee Formation.

Comments. *Fusispirifer* is abundant in the Permian of Western Australia (Archbold & Thomas 1987) and the present material indicates the presence of the genus in the Wooramel assemblages. The species is characterised by coarse costae and lateral plications that are variable but usually well developed on juvenile specimens but are poorly developed on the flanks of mature specimens. The Callytharra Formation species *F. carnarvonensis* possesses lower and usually finer ventral valve costae and very subdued lateral flank plications when compared with the material to hand. The younger *F. byroensis* (Glauert) (see Archbold & Thomas 1987) is a distinct flattish species readily distinguished from the Wooramel Group species.

A distinctive internal feature of the Wooramel species is the large, relatively wide ventral muscle field recalling that of the large species *F. wandageensis* from the late Early Permian Wan-

dagee Formation. The Wooramel specimens are closest to *F. carnarvonensis* from the Callytharra Formation but are distinct from that species and with the collection of additional material, particularly dorsal valves, will require the recognition of a new species.

Genus *Neospirifer* Fredericks, 1924

Type species. *Spirifer fasciger* von Keyserling, 1846.

Neospirifer sp.

Fig. 4H–J

Neospirifer sp.—Konecki et al. 1958: 33.—Condon 1962a: 11.—Condon 1967: 114.—McGann 1976: 51.

Neospirifer sp. B.—Archbold & Thomas 1986: 150, fig. 14 B, C.

Material. One natural cast of a ventral valve interior and one incomplete external mould of a ventral valve (CPC 19898–19899) from BMR locality 7864 0427, and one incomplete external mould of a ventral valve (CPC 24362) from BMR locality WB 69; all from the basal One Gum Formation.

Comments. As noted by Archbold & Thomas (1986: 150), the Wooramel *Neospirifer* species is related to the Western Australian *N. hardmani*–*N. plicatus* group of *Neospirifer* and appears to represent an intermediate species between the Callytharra and Madeline Formation species. The new material includes a fragment of a mature ventral valve (CPC 19899) which recalls specimens of an undescribed species of *Neospirifer* from the Aktastinian High Cliff Sandstone of the Perth Basin.

Order ATHYRIDIDA Dagys, 1974

Suborder ATHYRIDIDINA Boucot, Johnson & Staton, 1964

Superfamily ATHYRIDACEA M'Coy, 1844

Family ATHYRIDIDAE M'Coy, 1844

Subfamily ATHYRIDINAE M'Coy, 1844

Genus *Cleiothyridina* Buckman, 1906

Type species. *Atrypa pectinifera* Sowerby, 1840.

?*Cleiothyridina* sp.

Fig. 4K

Comments. A single specimen (CPC 24510) of an incomplete natural cast of a juvenile ventral valve interior from BMR locality 7864 0427 may represent an athyrid such as *Cleiothyridina*, judging from what appear to be traces of vascu-

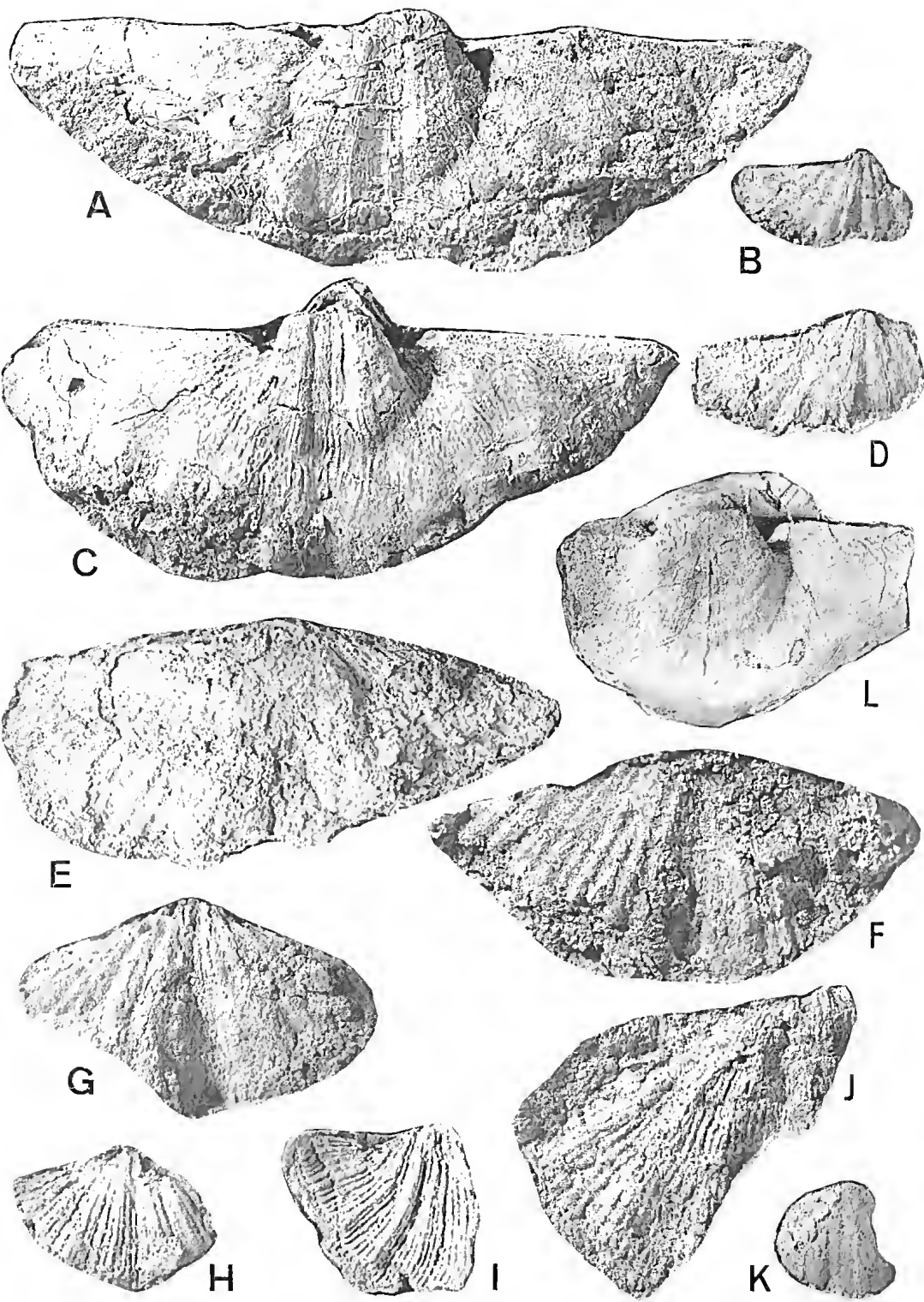


Fig. 4. A-G, *L. Fusispirifer* sp. A, CPC 19894, internal mould of ventral valve, $\times 1$. B, CPC 24506, latex cast of natural cast of juvenile ventral valve interior, $\times 1.5$. D, CPC 24507, latex cast of natural cast of juvenile ventral valve interior, $\times 1.5$. C, CPC 19895, internal mould of ventral valve, $\times 1$. E, CPC 19896, latex cast of ventral valve external mould, $\times 1$. F, CPC 24508, latex cast of ventral valve external mould, $\times 1$. G, CPC 24509, latex cast of ventral valve external mould, $\times 1$; note that lateral valve extremities are not preserved. L, CPC 19897, internal mould of ventral valve, $\times 1$. H-J, *Neospirifer* sp. H, CPC 19898, latex cast of natural cast of juvenile ventral valve interior, $\times 1.5$. I, CPC 24362, latex cast of ventral valve external mould, $\times 1$. J, CPC 19899, latex cast of incomplete ventral valve external mould, $\times 1.2$. K, ?*Cleiothyridina* sp., latex cast of natural cast of ?juvenile ventral valve interior, $\times 1.5$.

lar impressions. The specimen is inadequate for detailed comment.

Phylum MOLLUSCA

Class BIVALVIA

Comments. For completeness, two small fragmentary specimens (GSWA F43852-43853) from GSWA locality 94217 are figured (Fig. 3Q-R). Judging from descriptions and illustrations of Western Australian Permian Bivalvia provided by Dickins (1963), both specimens probably represent pectinaceans referable to *Aviculopecten*, *Etheripecten* or a closely related genus and appear close to forms from the Callytharra Formation.

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THE EFFECT OF LOW ROOT TEMPERATURES ON THE GROWTH OF MOUNTAIN FOREST EUCALYPTS IN RELATION TO THE ECOLOGY OF *EUCALYPTUS NITENS*

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To compare the response of four montane eucalypts to low soil temperature, seedlings of *Eucalyptus regnans*, *E. delegatensis*, *E. fastigata* and four provenances of *E. nitens* were treated for 100 days in a glasshouse. Mean ambient air temperatures varied between 15°C and 29°C while temperatures within the root zone were held in the vicinity of either 5°C or 10°C.

All species grew significantly better at the higher temperature for all variables measured. Differences in stem diameter, root length, root and shoot dry weight were consistent between species at both temperatures. Growth of *E. regnans* and *E. nitens* was similar overall. For most variables both species grew significantly better than *E. delegatensis*, which grew significantly more than *E. fastigata*. For height growth there was a highly significant interaction between species and temperature. At both temperatures, *E. regnans* made significantly better height growth than all other species. At the higher temperature, *E. fastigata* grew significantly taller than *E. nitens* and *E. delegatensis* but, at the lower temperature, *E. nitens* grew significantly taller than *E. delegatensis* and *E. fastigata*. Comparing the difference in height growth, *E. fastigata* and *E. delegatensis* were reduced substantially more than *E. nitens* by the cool root environment.

Eucalyptus nitens has a restricted distribution for a species with outstanding vigour. This may be related to a fire regime which also encourages the development of rainforest understoreys, and cool, heavily shaded soils. The implications of topography and fire regime on understorey type and soil temperature are discussed in relation to the ecology of *E. nitens*.

FOUR TALL forest eucalypts in the mountain forests of southeastern Australia have overlapping distributions in regions with mean annual rainfall exceeding 750 mm. *Eucalyptus delegatensis* R. Baker and *E. regnans* F. Muell are dominant species over extensive highland areas of Tasmania and Victoria (Eldridge 1972, Boland & Dunn 1985). *E. delegatensis* extends into southern New South Wales, replacing *E. regnans* above 1000 m over the greater part of its range. *E. nitens* (Deane & Maiden) Maiden and *E. fastigata* Deane & Maiden occupy similar latitudes in northern New South Wales (Sherry & Pryor 1967, Tibbits & Reid 1987). Both species extend south into East Gippsland, Victoria, while scattered stands of *E. nitens* also occur westward along the Great Dividing Range and into the Central Highlands. The elevation range of both species is influenced by latitude but, in Victoria, optimum development occurs at or near the lower limit of winter snow.

The growth rates of *E. nitens* are recognised as being greater than those of *E. regnans* in plantations up to 15 years (Pederick 1976), and planting trials indicate that *E. nitens* can be successfully grown in cool mountain areas receiving an annual rainfall of over 1000 mm (Turnbull & Pryor 1978). Despite this, the natural distribution consists mainly of small, disjunct stands (Pederick 1979) that may be enclaves of formerly more widespread populations.

Three broad regional forms of *E. nitens* have been recognised on the basis of leaf shape (Shepherd et al. 1976). The northern New South Wales form occurs near Mt Ebor and Barrington Tops. The southern New South Wales and West Gippsland forms both occur in Victoria. They differ in their morphology and vigour (Pederick 1979) and in some aspects of their physiology (Pederick & Lennox 1979, Tibbits & Reid 1987). The West Gippsland form is fast growing with strongly glaucous juvenile leaves and occurs

predominantly in the Central Highlands. The southern New South Wales form is less glaucous, less vigorous and has marginal glands on its mature leaves. The major occurrence of this form is on Errinundra Plateau. It also occurs intermixed with the West Gippsland form on the western slopes of the Baw Baw Ranges and on the Toorongo Plateau; however, the West Gippsland form does not occur naturally in East Gippsland.

In the Victorian Central Highlands, *E. nitens* is often found in association with or in close proximity to the cool temperate rainforest species *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. Mixed forest associations with *Elaeocarpus holopetalus* F. Muell and *A. moschatum* replace *N. cunninghamii* in East Gippsland beyond the natural range of that species. In areas where the understorey consists of a dense growth of *A. moschatum*, *E. holopetalus* and associated cool temperate closed forest species, an almost complete dominance of the site by *E. nitens* is often apparent. In northern New South Wales, mixed forest reoccurs with associations between *E. nitens* and *Nothofagus moorei* (F. Muell) Krasser (Pederick 1977).

The development of cool temperate closed forest understoreies has been associated with crown die-back in mature *E. delegatensis* forest in Tasmania (Ellis 1964, 1971, Ellis et al. 1980) although associated *E. dalrympleana* Maiden was unaffected. Ellis et al. (1980) concluded that depressed root temperatures due to the encroachment of closed forest may be important in the "decline" of *E. delegatensis*, as the deterioration could be reversed by cutting or burning

the understoreies. A mean annual soil temperature below 7°C was identified as the critical point at which the growth of *E. delegatensis* deteriorated (Ellis 1971). Although healthy and unhealthy stands differed little in winter soil temperatures, unhealthy stands had summer temperatures below 10°C. This suggested that soil temperature could be an important factor influencing the natural distribution of eucalypts (Ellis 1971).

The strong topographic and floristic similarities between the declining *E. delegatensis* forests of Tasmania and the apparently unaffected *E. nitens* forests of Errinundra Plateau suggested that *E. nitens* might be more tolerant of low soil temperatures than *E. delegatensis*. This factor might also influence the distribution of *E. regnans* and *E. fastigata* in eucalypt-rainforest associations in Victoria. The aim of this study was to test this experimentally under controlled conditions.

METHOD

To investigate the effect of lowered root temperatures on eucalypts occurring in the montane zone and likely to form an association with a rainforest understorey, seedlings of four common montane eucalypts were grown at temperatures near that identified by Ellis (1971) as critical to the onset of die-back. Seedlings for the trial were grown from provenances listed in Table 1. Seeds of *E. nitens* were collected from several trees at each provenance and care was taken to distinguish between the southern New South Wales and West Gippsland forms at Mt Toorongo. Seeds of *E. delegatensis*, *E. fastigata* and *E. regnans* came from bulked seed lots and

Species	Locality	Latitude	Longitude	Elevation (m.a.s.l)	Form
<i>E. nitens</i>	Royston River, Central Highlands	37° 25'	146° 53'	1000	West Gippsland (CR)
<i>E. nitens</i>	Mt Toorongo, Central Highlands	37° 50'	146° 07'	1200	West Gippsland (CT)
<i>E. nitens</i>	Mt Toorongo, Central Highlands	37° 49'	146° 07'	1000	Southern NSW (ET)
<i>E. nitens</i>	W Errinundra, East Gippsland	37° 19'	148° 52'	1000	Southern NSW (EE)
<i>E. delegatensis</i>	Delegate River, East Gippsland	37° 17'	148° 50'	1000	East Gippsland
<i>E. fastigata</i>	Delegate River, East Gippsland	37° 17'	148° 50'	1000	East Gippsland
<i>E. regnans</i>	Nunnet, East Gippsland	37° 14'	148° 05'	1000	East Gippsland

Table 1. Eucalypt species and provenance.

would have included a greater number of parent trees.

A selection of uniformly large seeds was germinated on moist plugs of sterile rock fibre. *E. delegatensis* was sown after 6 weeks stratification at 4°C. Because of greater growth rate of seedlings, seeds of all other species were sown one month later. Five seeds were sown in each plug. After germination each plug was placed on the top of a 250 mm length of 60 mm diameter PVC pipe filled with clean river sand. The seedlings were kept moist in a shade house by spray irrigation and fertilized every third day with 10 mL of water and 10 mL of Duralite Hysol, a complete hydroponic nutrient solution. Once established, the seedlings were thinned to leave one plant within each growth tube.

After 115 days from the first sowing, the plants were transferred to an empty glasshouse where they were temporarily stored on the floor. After measuring plant height, ten individuals of each provenance were randomly chosen for initial dry weight and root length determination. At this stage the *E. nitens* seedlings developed a light infection of powdery mildew. All plants were elevated on benches and given two applications of TILT (Ciba-Geigy), a wide spectrum Triazole derivative systemic fungicide at a five day interval. Within ten days there was no evidence of active infection. The plants were given a further 20 days to recover and acclimatise to the glasshouse before the cool root treatment was applied. During this period all seedlings were showing healthy and apparently unaffected new growth. The *E. delegatensis* seedlings were therefore 145 days old at the commencement of the experiment.

Two root temperatures were replicated three times, in six forced air coolers. Mean warm root temperatures were maintained between 8.5°C and 10.5°C while mean cool root temperatures were maintained between 4.5°C and 6.5°C. Temperatures were measured using mercury thermometers inserted to a depth of 75 mm at both

ends of the cooler. The treatments were arranged down the centre of the glasshouse so that the different root temperatures were adjacent. Five plants of each of seven provenances were allocated at random to each of the six coolers. The plants were evenly distributed with their centres 110 mm apart.

The growth tubes were suspended through a false lid so that the roots in each tube were surrounded by fan-circulated air at controlled temperature, while the aerial parts of each plant were exposed to the ambient temperature of the glasshouse. A small temperature gradient of approximately 1°C existed across each cooler, and small differences in the operation of thermostats meant that the regulation of root temperature differed slightly between coolers. To compensate, lids were moved between coolers and turned once through 180° within each cooler so that, as far as possible, all plants experienced an equivalent root and shoot environment.

Temperature control in the coolers was adequate to ensure that clear differences existed between treatments and that similar temperatures were maintained between replicates (Table 2). Some difficulties were experienced in adjusting the thermostat in cooler 1 and the cooler was replaced after 16 days. Cooler 6 failed over a weekend and was replaced the following Wednesday. Typically, temperature fluctuates in the upper soil horizons both diurnally and annually, and lags behind air temperature. Experimentally maintained constant temperatures do not mimic most natural situations, although they may be more typical of soils protected by dense, rainforest vegetation. Watson (1980) considered that soils above 400 m elevation of the Great Dividing Range of Victoria are likely to have a mean annual temperature between 8°C and 15°C. On Errinundra Plateau at mid morning in mid November, soil temperatures of 7–8°C were obtained using a mercury thermometer at 130 mm depth, beneath dense rainforest vegetation. It is therefore conceivable that the experimental

Treatment Temp (°C)	Cooler	May/June (°C)	July (°C)	Period	May/Sept (°C)
				Aug/Sept (°C)	
10°C	1	9.8–12.5	8.6–9.5	8.9–9.6	9.1–10.5
	3	9.6–10.7	8.2–9.4	8.5–9.6	8.8–9.9
	5	9.4–11.8	8.5–9.4	8.8–9.9	8.9–10.4
5°C	2	4.8–6.3	4.5–6.7	4.8–6.1	4.7–6.4
	4	5.1–6.1	4.4–5.0	5.0–6.0	4.8–5.7
	6	6.2–7.4	4.6–5.5	4.4–5.8	5.1–6.2

Table 2. Mean minimum and maximum soil temperature in each cooler.

temperatures could be experienced naturally by the species involved in the trial.

The root medium was washed with water and the plants fertilized to excess every second or third day, initially with 60 mL of nutrient solution, then with 120 mL as they increased in size. Glasshouse temperature and humidity were monitored by a continuous recording thermo-hydrograph. Occasional roots extending beyond the growth tubes were clipped and stored in an alcohol and formalin mixture. Fallen leaves were collected for dry weight determination.

The trial ran for 100 days after which plants were measured for diameter at the harvest point (Dia) and total height (Ht). After harvest, the roots were placed on a fine wire mesh and washed free of sand by a gentle spray and hand teasing, with final cleaning of attached sand grains by forceps. They were stored in an alcohol/formalin mixture for root length determination. Total root length (RL) was determined using a Comair Rootlength Scanner (Richards et al. 1979). Root lengths estimated to be greater than 100 m were partitioned for separate measurement. Roots and shoots were held at 65°C for five days and dry weights of root and shoot (Dwt(r), Dwt(s)) were determined after stabilising for 1 hour at room temperature.

RESULTS

Mean monthly air temperature and relative humidity in the glasshouse during the trial (Table 3) were uniform, with a diurnal fluctuation in mean maximum and minimum temperature of 10°C and in relative humidity of

approximately 20–30%. Absolute maximum and minimum temperatures of 37.7°C and 11.2°C were recorded.

Increment in growth was obtained by subtracting initial values for each plant in the case of height, and means of an initial sample for root length and dry weight of roots and shoots. An analysis of variance showed all variables to be significantly affected by temperature (Table 4), with growth reduced at the lower soil temperature, as expected.

Height was the only variable for which a temperature \times species interaction was significant and this was highly significant (Table 4). At the higher temperature, height growth of *E. regnans* and *E. fastigata* was significantly greater than *E. nitens* and *E. delegatensis* ($p < 0.01$) which were not significantly different from each other. At the lower root temperature, height growth of *E. nitens* was significantly greater than that of *E. delegatensis* or *E. fastigata* ($p < 0.001$). At 5°C, height growth of both *E. delegatensis* and *E. fastigata* was ca. 60% less than that at 10°C. In contrast the height reduction in *E. regnans* and *E. nitens* was ca. 30% or less (Table 5). *Eucalyptus regnans* achieved much better height growth at both temperatures at this age than all other species (Table 5). At both temperatures, the southern New South Wales form of *E. nitens* grew significantly better than the West Gippsland form ($p < 0.01$), and within forms there was no significant difference between provenances.

A comparison of shoot to root ratios at the two temperatures (Table 6) suggests that *E. nitens* and *E. regnans* differed from *E. delegatensis* and *E. fastigata* in their ability to maintain stronger shoot growth relative to root growth at the lower

Period	Mean Temperature (°C)		Mean Relative Humidity %	
	Maximum	Minimum	Maximum	Minimum
May–June	26.5	16.5	67.0	43.1
July	27.2	17.6	67.3	46.4
Aug–Sept	29.1	15.1	72.7	40.6

Table 3. Mean monthly air temperatures and relative humidities in the glasshouse.

Variable	Height	Diameter	Root Length	Dry Weight Shoot	Dry Weight Root	Dry Weight Total
Temp.	0.007	0.023	<0.001	0.011	0.005	0.009
Temp. \times Species	<0.001	0.353	0.433	0.893	0.342	0.822

Table 4. Probability values from analysis of variance testing the effect of soil temperature and temperature/species interactions. The main effect of species was significant at $p < 0.001$ for all variables.

Species	Mean Height Increment (mm) Soil Temperature		Percentage Reduction in Height Growth with fall in Soil Temperature
	5°C	10°C	
<i>E. nitens</i> CR	299	440	32
<i>E. nitens</i> CT	277	403	31
<i>E. nitens</i> EE	364	500	27
<i>E. nitens</i> ET	395	481	18
<i>E. regnans</i>	436	630	31
<i>E. delegatensis</i>	160	406	61
<i>E. fastigata</i>	204	546	63
Least Significant Difference	67	66	

Table 5. Comparison of mean shoot height increment (mm) during the experimental period at two soil temperatures.

Species	Shoot(g)/Root(g) Soil Temperature			Shoot (mm)/Root (m) Soil Temperature		
	5°C	10°C	Difference	5°C	10°C	Difference
<i>E. nitens</i> CR	4.5	4.0	0.5	2.8	2.5	0.3
<i>E. nitens</i> CT	4.9	4.6	0.3	5.2	4.1	1.1
<i>E. nitens</i> EE	4.5	4.7	-0.2	5.2	4.7	0.5
<i>E. nitens</i> ET	4.2	3.9	0.3	5.1	4.1	1.0
<i>E. regnans</i>	5.2	4.6	0.6	6.9	4.9	2.0
<i>E. delegatensis</i>	3.8	4.2	-0.4	2.5	3.9	-1.4
<i>E. fastigata</i>	3.6	4.1	-0.5	6.8	7.2	-0.4

Table 6. Ratio of mean shoot to root dry weight growth and increment in length, and their differences at the two soil temperatures.

temperature. Comparatively low and high root lengths were responsible for the high and low length ratios for *E. fastigata* and the Royston provenance of the West Gippsland (CR) form of *E. nitens* respectively.

For those variables where there was no significant interaction between species and temperature, the data from the different temperatures were combined to determine the significance of difference between species (Table 7). *E. nitens*

overall grew significantly better ($p < 0.05$) than *E. delegatensis* for all variables, and the growth of *E. delegatensis* was significantly greater than *E. fastigata* for all variables ($p < 0.001$). The West Gippsland form of *E. nitens* from Royston (CR) grew significantly better than *E. regnans* and the other provenances of *E. nitens* for all variables. *E. regnans* was significantly better than *E. delegatensis* for all variables except root length and basal stem diameter.

Variable Temp°C	Basal Stem Diameter (mm)			Total Root Length (mm)			Shoot Dry Weight (g)			Root Dry Weight (g)			Total Dry Weight (g)		
	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean
<i>E. nitens</i> CR	0.54	0.60	0.57	108	173	141	5.97	8.77	7.37	1.33	2.20	1.77	7.31	10.96	9.14
<i>E. nitens</i> CT	0.43	0.54	0.48	53	99	76	3.40	5.89	4.65	0.70	1.27	0.99	4.10	7.16	5.63
<i>E. nitens</i> EE	0.46	0.55	0.51	70	106	88	4.73	6.97	5.85	1.05	1.48	1.27	5.79	8.45	7.12
<i>E. nitens</i> ET	0.51	0.57	0.54	77	117	98	5.09	7.31	6.20	1.20	1.87	1.54	6.29	9.19	7.74
<i>E. regnans</i>	0.44	0.52	0.48	63	129	84	4.57	7.63	6.15	0.87	1.66	1.28	5.44	9.30	7.44
<i>E. delegatensis</i>	0.38	0.51	0.45	64	103	84	2.98	5.64	4.31	0.79	1.33	1.06	3.77	6.97	5.37
<i>E. fastigata</i>	0.27	0.40	0.33	30	76	53	1.46	3.53	2.46	0.41	0.87	0.63	1.88	4.40	3.10
Least Significant Difference			0.04			17			0.80			0.21			0.98

Table 7. Mean growth at each soil temperature for variables in which the species \times temperature interaction was not significant, and combined temperature means for each species.

DISCUSSION

Although the effect of low root temperatures has been widely researched in horticulture (e.g. Cooper 1973, Nielsen & Humphries 1966), the implications of low soil temperatures on growth have received little consideration in the study of natural ecosystems. Low soil temperatures influence the formation of mycorrhizal associations (Theodorou & Bowen 1970) and increase the resistance to the uptake of nutrients (Kramer 1969). In particular, phosphorus is absorbed much more slowly at low than at high temperatures (Sutton 1969). Paton et al. (1979) observed the effect of root temperature on dehardening of four species of eucalypts and found that root temperature in the range 0.5–1.0°C delayed the dehardening response of warm shoots. In general, below the optimum temperature, height growth, root length and dry weight production show a broad sigmoidal increase with increasing temperature to an optimum, beyond which further temperature increase causes a decline in productivity. In most trials of horticultural or agricultural species, the optimum band of root temperature differed between species but was between 20–30°C. In this trial, root temperatures were probably well below optima for all species.

The significant interaction between species and temperature for height growth in this trial was not evident for the other variables tested. Eucalypts that compete with vigorous shrub growth in the early stages of establishment must make rapid, early height growth if they are to survive. In contrast, diameter growth changes little, particularly during the seedling stages. Thus height growth of seedlings may be more sensitive to the different root temperature regimes than the other variables tested. A similar discrepancy between height growth and dry weight production was recorded for *Pinus radiata* and *Pinus contorta* by Sweet & Wareing (1968). Dry weight of their second year seedlings was almost identical for the first eight months, despite more than 30% difference in height growth. In the following months, when the height growth of both species was negligible, dry weight production continued at a reduced rate and clear differences were finally evident in the partitioning of dry weight between root and stem. For the eucalypts tested in this trial, soil temperature appeared to influence this ratio with the response of *E. regnans* and *E. nitens* differing from that of *E. fastigata* and *E. delegatensis*.

The height growth of the southern New South Wales form (EE and ET), which was significantly better than the West Gippsland form (CR and CT), emphasises the difficulties associated with using seedlings as a guide to growth in later stages (Table 5). Pederick (1979) found ranking of provenances according to height growth changed after planting in the field. The Errinundra provenance which was initially the tallest had become the shortest within three years. Thus the growth of seedlings in containers is at best a poor guide to the response of mature to over mature trees growing in the natural environment.

Major Victorian occurrences of *E. nitens* are on plateaus. At the time of European settlement the most extensive populations of *E. nitens* occurred on Errinundra Plateau and Toorongo Plateau. Where the species occurs amongst more steeply dissected land forms, it is often confined to depressions, gully heads or on moderate slopes, in contrast to forests of surrounding species, eg. Connors Plains, Mt Useful Spur, headwaters of Snobs Creek, Moroka, Royston, Rubicon, Little and Taggerty Rivers, Torbreck Range (Pederick 1977) and slopes below the Baw Baw Plateau, e.g. Christmas Creek.

Plateau topography affects at least two factors that influence the vegetation. The undulating landform may increase the severity of frosts through cold air drainage, and by influencing the rate of fire spread, plateaus may reduce fire intensity and frequency.

Where the effect of frost is regular and pronounced it may delimit the tree line (Moore & Williams 1976). Rare but exceptionally severe frosts may influence the segregation of species (Davidson & Reid 1985), particularly amongst lower growing species. For tall growing eucalypts, frost effects are likely to be most severe during early establishment stages. Superior frost resistance combined with good growth rate has led to the increasing significance of *E. nitens* as a plantation species in Tasmania (Tibbitts 1986) and in other countries (Tibbitts & Reid 1987). High frost frequency on Errinundra Plateau could be at least partly responsible for that extensive occurrence of *E. nitens* (Featherstone et al. 1987), although a comprehensive study of variation in frost resistance indicated that the southern New South Wales and Errinundra provenances of *E. nitens* were least frost hardy (Tibbitts & Reid 1987). Damage due to frost would be most pronounced during early regeneration stages, particularly if regeneration occurred as even aged stands without the pro-

tection of an overwood. Since 1967, 4800 ha of forest have been logged by clear felling on Errinundra Plateau. Because of limited seed production, it has not been possible to regenerate these stands with pure *E. nitens*. Various mixtures of *E. nitens*, *E. delegatensis* and *E. fastigata* have been used, with extensive areas regenerated by a seed mixture containing equal proportions of all three. To date regeneration of all three species has occurred without a particular problem due to frost.

Because fire intensity is exponentially related to slope (McArthur 1967) fires burn less intensely on plateaus, and possibly less frequently. The multi-aged stands observed in Tasmania (Webb et al. 1983) are favoured on plateaus because fires create favourable seed bed conditions but have less tendency to destroy the overwood, particularly where this consists of mature trees. Forests with these structures have been observed over a long period in *E. regnans* and *E. delegatensis* forests in Victoria and Tasmania (Lindenmayer et al. 1990). Similar structures have been recorded in mixed stands of *E. nitens* and *E. delegatensis* in the headwaters of the Rodger River (Chesterfield et al. 1983), and in *E. nitens* on Errinundra Plateau. Fires in 1939 burnt the margins of Errinundra Plateau and, at one point where the regrowth occurred amongst a scattered stand of *E. nitens*, the multi-aged structure is clearly evident (Chesterfield et al. 1988). More recently, during burning of logging debris on Errinundra Plateau, approximately one hectare of mature forest recovered after complete defoliation by heat scorch. Thus, provided adequate gaps occur, the formation of multi-aged stands is not an improbable event.

The modification of the fire regime by plateau topography that favours the formation of multi-aged eucalypt stands also protects and encourages the development of rainforest in areas where soils and rainfall are adequate. In Victoria, *Atherosperma moschatum*, *Nothofagus cunninghamii* and *Elaeocarpus holopetalus* are important constituents of the *E. nitens* environment and, in the absence of fire, produce heavily shaded soils at maturity. Forests with similar composition and structure occupy similar environments in Tasmania. Here somewhat uneven aged stands of *E. delegatensis* first declined in the early 1960s, following a period of approximately 140 years without fire. Die-back was associated with the development of dense, closed forest understories. Trees of all age classes and canopy positions were affected and the onset of die-back was influenced by elevation.

Below 750 m, stands with a similar understorey were unaffected. After studying soil chemical factors, Ellis & Graley (1987) concluded that the small differences were more likely to be the result rather than the cause of successional changes. Ellis (1971) initially proposed that temperature changes in the root environment were a possible explanation. Over a two year period he recorded mean annual soil temperatures at a depth of 450 mm which were 2–3°C higher under grass in comparison with the rainforest understorey. After considering the environmental lapse rate he calculated that the rainforest invasion was equivalent to an altitudinal increase of 335–520 m, placing stands at 915 m, well above their altitudinal limit. Although the cause of die-back has not been ascertained with any certainty, the results for height growth in this study support the hypothesis that low soil temperatures may be a factor contributing to the decline in *E. delegatensis*. The natural post fire succession in this forest type is toward understories that are open at maturity and dominated by grasses, forbs, and ferns over the greater part of their range. Heavily shaded soils associated with a closed forest understorey are rarely present.

The similarities between the vegetation, fire regime and successional changes that have occurred on the elevated montane plateaus of Victoria and Tasmania are striking, with the exception that in Victoria, in areas where the rainforest understorey is dense, die-back of the *E. nitens* overstorey has not been observed. It is recognised that *E. nitens* can tolerate the incursion of rainforest species for longer periods than either *E. delegatensis* or *E. regnans* (United Nations Food and Agriculture Organisation 1979).

In the montane forests of southeastern Australia, fires over a wide elevation zone extending above and below the snow line have been sufficiently frequent to favour eucalypt species capable of producing regular and reliable seed crops. Although *E. nitens* has proven to be of equal or superior vigour to most of its competitors in growth trials, it is an unreliable and poor seed producer (United Nations Food and Agriculture Organisation 1979, Turnbull & Pryor 1978, Boland et al. 1980), particularly when compared to *E. regnans*, *E. delegatensis* and *E. fastigata*. Therefore, as the frequency of fire increases, the proportion of *E. nitens* in mixed stands is likely to decline, as noted in the Rodger River (Chesterfield et al. 1983).

The role of fire in the natural distribution of *E.*

nitens may resemble that of *E. grandis* Maiden, another eucalypt that associates with rainforest genera (Cromer 1960). The natural distribution of *E. grandis* is restricted to moist gullies or tablelands (Turnbull & Pryor 1978) due to its extreme sensitivity to fire (Pryor 1972). In the event of a change in fire regime to provide greater protection, the range of *E. grandis* may be readily extended into adjoining sites. Conversely, an increase in the frequency and intensity of fire would cause a contraction of the range. Ashton (1981) considered that during the Pleistocene fires may have been much rarer events than at present, and that the wet sclerophyll forests may have been relatively scarce ecotones between rainforests and the more drought resistant eucalypt forests or woodlands. As fire increased with increasing aridity during the early Quaternary, the contraction of rainforest may have enlarged the ecotone as fire reduced or modified rainforest over the greater part of its range. Some species of *Encalyptus*, *Tristaniopsis* and some rainforest genera adapted to regenerate following disturbance, or on marginal sites, e.g. *Arancaria*, *Flindersia* (Cromer & Pryor 1942), may have dominated this ecotone. The co-existence of eucalypts with cool temperate closed forest has been suggested in areas of Tasmania where fire is infrequent but sufficiently frequent (intervals less than 350 years) to maintain the eucalypts (Gilbert 1959). Thus the fire regime during the early Quaternary may have contributed to vegetation with similar structure to the mixed forest surviving on Errinundra Plateau, and in other isolated montane and coastal forests of southeastern Australia.

After the arrival of the Aborigines, a sudden and dramatic increase in fire frequency may have allowed eucalypts to expand into moister sites that they had not formerly occupied (Smith & Guyer 1983). In southeastern Australia, species belonging to the subgenus *Monocalyptus* are frequently best adapted to such sites (Florence 1981). Their more recent evolution on uniform, regularly watered sites may explain a tendency to form monospecific stands in tall open-forests, lower tolerance to prolonged water stress and their restriction to higher rainfall zones in the south-east and south-west of the continent. The expansion of fire-adapted species may have seen a contraction of rainforest and mixed forest dominated by eucalypts adapted to long intervals between fires. The contraction would have occurred last in the most fire protected localities. In some areas of Victoria,

elevation and topography appears to have been important for the survival of *E. nitens*.

At elevations below the limit of permanent winter snow, *E. nitens* is in competition with *E. regnans* and *E. fastigata* and at higher elevations with *E. delegatensis*. In general, its competitors produce reliable, heavy seed crops and regenerate prolifically after hot fires. In contrast, *E. nitens* produces light and irregular seed crops, and over a long period a series of hot fires could be expected to cause a progressive diminution in its abundance. In competition with *E. regnans*, a species of comparable vigour, the decline in *E. nitens* would be appreciable after each regeneration phase. The ability of *E. nitens* to compete with *E. delegatensis* is limited by the dormancy characteristics of its seed. The stratification requirement of *E. delegatensis* seed indicates an adaptation to an environment where snow may lie for extended periods during winter (Boland et al. 1980). Without this adaptation, the mortality of *E. nitens* germinants would be high, restricting the upper limits of natural establishment to elevations where snow generally persists for less than several weeks. This environment coincides with the extremes in distribution for *E. delegatensis* and *E. regnans*, allowing *E. nitens* to exploit the ecotone where both its competitors are at the limits of their range. The occurrence of plateau land form at this vulnerable point in the elevation gradient of both *E. regnans* and *E. delegatensis* may have protected the niche available to *E. nitens* by a modification of the fire regime. On plateaus, fires occur less intensely and probably less frequently, favouring the development of multi-aged stands. In forests with this structure, poor seed production would have been much less critical to species survival, and competitors promoted by fire less invasive. The fire regime occurring on plateaus also favours the development of rainforest understoreies. An ability to co-exist at various times for extended periods in this association, may have been a factor in the survival of *E. nitens* on plateau and gully topography in Victoria.

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THE TASMANIAN MUDFISH, *GALAXIAS CLEAVERI* SCOTT, 1934, IN VICTORIA

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KOEHN, J. D. & RAADIK, T. A., 1991:12:31. The Tasmanian mudfish, *Galaxias cleaveri* Scott, 1934, in Victoria. *Proceedings of the Royal Society of Victoria* 103 (2): 77-86. ISSN 0035-9211.

Galaxias cleaveri Scott, 1934 is recorded for the first time from the Aire River basin in western Victoria, extending the known westerly distribution of the species. The habitat, general biology and behaviour of the species are described and comparisons made with three species of New Zealand mudfish (*Neochanna* spp.). *G. cleaveri* is nocturnal and able to survive periods without free surface water. Large areas of potential *G. cleaveri* habitat have been destroyed in Victoria, and the preservation of freshwater wetland habitats is essential to the survival of the species in this State, where a conservation status of vulnerable remains justified.

THE TASMANIAN MUDFISH, *Galaxias cleaveri* Scott, a member of the southern hemisphere family Galaxiidae, is a scaleless salmoniform fish first described from Tasmania in 1934 although specimens had been dug up at Strahan in western Tasmania in 1900 (Hall 1901, Scott 1934). The species was considered endemic to Tasmania until 1980 when specimens were discovered on mainland Australia (Jackson & Davies 1982). In the 56 years since its discovery *G. cleaveri* has been recorded only spasmodically, an indication that it is rare in terms of distribution and abundance. Consequently little is known of the general biology and ecology of this species; indeed, not until 1986 did anyone report that it possesses a marine larval stage (Fulton 1986). In the present paper we highlight the presence of *G. cleaveri* in Victoria and provide updated information to help further work and the development of management strategies.

Detailed descriptions of *G. cleaveri* were given by Andrews (1976), McDowall & Frankenberg (1981) and Cadwallader & Backhouse (1983), and the last authors provided a colour photograph. Even so, workers less skilled in the taxonomy of fish may experience difficulty in distinguishing *G. cleaveri* from the broad-finned galaxias, *Galaxias brevipinnis* Günther, and the mountain galaxias, *Galaxias olidus* Günther, which may occur within the same river system.

The following morphological features may be used as a simplified guide to distinguishing adult *G. cleaveri* from *G. brevipinnis* and *G. olidus* (Fig. 1).

1. Anal fin slightly behind origin of dorsal fin in *G. cleaveri*.
2. Shape of dorsal and anal fins: low, rounded to ovoid, elongated posteriorly in *G. cleaveri*.
3. Shape of caudal fin: rounded to truncated in *G. cleaveri*.
4. Shape of flanges on caudal peduncle: large, long and raised in *G. cleaveri*.
5. Shape of pectoral fins: large and rounded in *G. cleaveri*.
6. Small head in *G. cleaveri*.
7. Size of eyes: small in *G. cleaveri*.
8. Large long tubular nostrils: more pronounced in *G. cleaveri*.

Morphological similarities are exhibited with three species of New Zealand mudfish (McDowall & Whitaker 1975, McDowall 1990): the Canterbury mudfish, *Neochanna burrowsius* (Phillipps) (Skrzynski 1968, Cadwallader 1975); the brown mudfish, *N. apoda* Günther (Eldon 1968, 1971); and the black mudfish, *N. diversus* Stokell (Thompson 1987, McDowall 1990). In habitat and habits *G. cleaveri* shows similarities to these species and to the dwarf galaxias, *Galaxiella pusilla* (Mack) (Backhouse & Vanner 1978, Beck 1985, Humphries 1986).

DISTRIBUTION

Previous records

G. cleaveri has been found to be patchily distributed in coastal areas in the north, south and west of Tasmania (Andrews 1976, McDowall & Frankenberg 1981, Fulton 1990) but was reported to be absent from Flinders and King

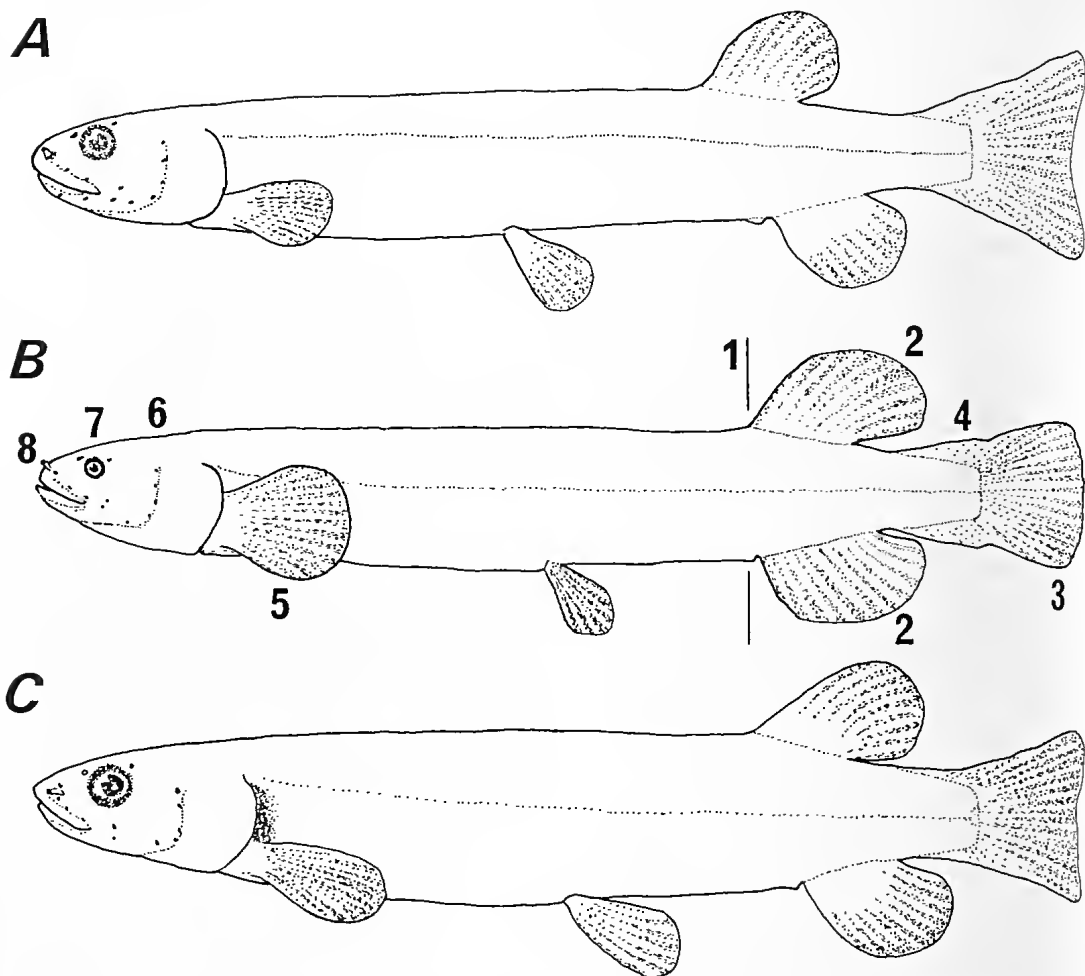


Figure 1. Morphological features distinguishing *Galaxias cleaveri* (B) from *G. olidus* (A) and *G. brevipinnis* (C). (After McDowall & Frankenberg 1981.)

Islands in the 1960s (Frankenberg 1967). Andrews (1976) was surprised at the absence of *G. cleaveri* from the Bass Strait islands and mainland Australia, even though at that time he did not know that the species possessed a marine juvenile stage.

G. cleaveri was first recorded on mainland Australia in 1980 from the south-east side of Wilsons Promontory, Victoria (Jackson & Davies 1982). In 1983 another individual was recorded from the lower reaches of the Wye River, Otway Ranges (Kochner & O'Connor 1990a; specimen NMV A7594, Department of Ichthyology, Museum of Victoria, Melbourne), extending the known range of the species into western Victoria. These two sites are referred to herein as sites 1 and 2 (Fig. 2, Table 1).

Subsequently, Green (1984) reported *G. cleaveri* from a drain on Flinders Island, Bass Strait (specimens QVM 1984/5/6, Queen Victoria Museum and Art Gallery, Launceston, and NMV A3391). This record completed a distribution pattern coinciding with that of other galaxiid species having a trans-Bassian distribution, namely *G. brevipinnis*, *G. maculatus* (Jenyns), *G. truttaceus* (Valenciennes) and *Galaxiella pusilla* (Frankenberg 1967).

It is not surprising that *G. cleaveri* has been recorded in only two of the numerous other surveys previously conducted to determine the distribution of freshwater fish in coastal Victoria (see Koehn 1990, Koehn & O'Connor 1990a, Koehn et al. 1991). Sites sampled during those surveys were mostly in streams rather than in

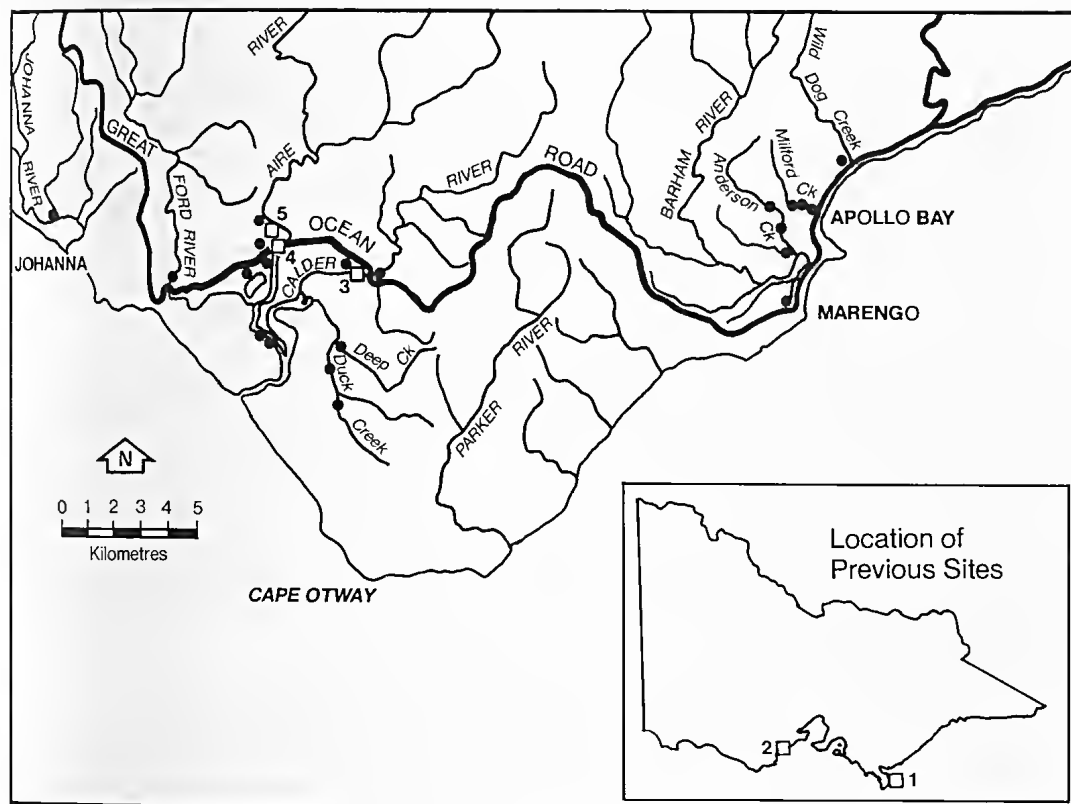


Figure 2. Localities from which *Galaxias cleaveri* has been recorded in Victoria (□); ● = additional sites surveyed in this study, but where *G. cleaveri* was not found. Inset: areas where *G. cleaveri* was previously recorded by Jackson & Davies (1982) (1) and Koehn & O'Connor (1990a) (2).

swamp and drain habitats favoured by this species. In addition, specimens of *G. cleaveri* may have been misidentified, particularly before the species was recognised as occurring in Victoria.

New records

In 1990 we surveyed likely *G. cleaveri* habitats (small creeks, drains and swamps) in the lowland coastal plains of the Otway Ranges between Skenes Creek (143°43'E, 38°43'S) and the Johanna River (143°23'E, 38°45'S) (Fig. 2). Twenty-four sites were sampled using a Smith Root Model 12 backpack electrofisher and dip nets. Details of all sites sampled and fish species collected are included in Koehn et al. (1991). Eleven specimens of *G. cleaveri* were collected from three sites (sites 3, 4 and 5; Fig. 2 and Table 1) in the Aire and Calder River valleys, 35 km west of the locality on the Wye River where the species was recorded by Koehn & O'Connor

(1990a). Specimens have been deposited with the Museum of Victoria: NMV A9512 (Calder River); NMV A9513, A9510 (Aire River, drain); NMV A9511 (Aire River, billabong).

Population density of *G. cleaveri* at the three sites could not be estimated because of the dense vegetation and because of the cryptic and nocturnal habits of *G. cleaveri*. The option of clearing aquatic vegetation to sample more effectively was rejected as all sites were small in area.

Associations

All other species associated with *G. cleaveri* (Table 1) are common in the area (Koehn & O'Connor 1990a), are diadromous (with the exception of *Pseudogobius olorum*), and most have been recorded from low-lying swampy habitats. *P. olorum* is usually resident in lower freshwater or estuarine areas as well as in coastal lagoons (Allen 1989), and the specimens of *G. brevipin-*

Site No.	Waterway	Map No. & Grid Ref.	Altitude (m)	Date Sampled	No. Collected	Total Length Range (mm)	Assoc. Species
1	Freshwater Creek ^A (tributary)	8119 493746	20	29.10.80 16.12.80	5 10	37-75*	Sfeel,Cgal
2	Wye River ^B	7620 514196	10	14.09.83	1	93*	Amm,Cgal,Agrayl, Tup,Btr
3	Calder River (drain)	7620 178056	20	17.10.90	1	90	Sfeel,Cgal
4	Aire River (drain)	7520 147063	10	31.05.90 24.08.90 17.10.90	2 5 2	56-57 74-96 85-90	Sfeel,Cgal Sgal,Bgal,Bsg —
5	Aire R (billabong)	7520 151068	15	16.10.90	1	80	—

amm = lamprey ammocoetes, *Geotria australis* or *Mordacia mordax*

Cgal = common galaxias, *Galaxias maculatus*

Sfeel = short-finned eel, *Anguilla australis*

Sgal = spotted galaxias, *Galaxias truttaceus*

Bgal = broad-finned galaxias, *Galaxias brevipinnis*

Tup = tupong, *Pseudaphritis urvillii*

Btr = brown trout, *Salmo trutta*

Agrayl = Australian grayling, *Prototroctes maraena*

Bsg = blue-spot goby, *Pseudogobius olorum*

^A from Jackson & Davies (1982)

^B from Koehn & O'Connor (1990a)

* standard lengths

Table 1. Summary of site and collection details for *Galaxias cleaveri* in Victoria.

nis collected were juveniles migrating upstream to adult habitat.

The association of eels and other species of galaxiids with New Zealand mudfish (*Neochanna* spp.) has been observed by Eldon (1968), and *G. cleaveri* has been associated with other galaxiids and with southern pygmy perch, *Nannoperca australis* Günther (Scott 1936, 1971).

In *G. cleaveri* habitats surveyed on mainland Australia the other resident galaxiid species are essentially free-swimming, whereas *G. cleaveri* is benthic. Thus *G. cleaveri* may face natural interspecific competition or predation only from eels which are also benthic and may occupy similar habitats.

Biogeography

The distribution of freshwater native fishes in the Otway region appears to be primarily related to geomorphological conditions that existed during and after the last glaciation 5,000–20,000 years ago (Koehn & O'Connor 1990a). Such conditions restricted non-diadromous freshwater species to the larger Barwon River system to the north and to the Aire and Gellibrand River systems to the south-west, whereas only diadromous species inhabit the short coastal streams.

The diadromous lifecycle of *G. cleaveri* accounts for its occurrence in the Wye River.

Frankenberg (1974) suggested that *G. truttaceus* and *G. brevipinnis*, both species with life-cycles similar to that of *G. cleaveri*, may have migrated to mainland Australia from Tasmania when a land bridge existed during the Pleistocene glaciation. A similar migration may be suggested for *G. cleaveri*. Fulton (1986) described a return to fresh water by juvenile *G. cleaveri* and suggested a marine phase in the species' lifecycle (Fulton 1990). The distribution and residency of the larval phase of *G. cleaveri* is unknown, as is the possibility of land-locked populations of the species not possessing a marine life phase. Such populations are known in other normally diadromous galaxiid species (Pollard 1972, Humphries 1989, Fulton 1990, McDowall 1990).

The present distribution of *G. cleaveri* closely conforms to the region encompassed by the land bridge (Wilson's Promontory to Cape Otway). Larvae developing in marine waters would be dispersed more widely and the species would be expected to be more widely distributed. The occurrence of larval galaxiids as far as 700 km from the coast of New Zealand supports the theory of McDowall (1978) that long-range dispersal of

diadromous species may occur, as is exhibited by *G. truttaceus* and *G. brevipinnis* which are widespread in Victorian coastal streams (Koehn & O'Connor 1990a, 1990c). The more restricted distribution of *G. cleaveri* suggests that the larvae may be confined to estuaries, although further surveys are needed to elucidate dispersal mechanisms.

HABITAT

A comprehensive description of the undisturbed habitat at site 1 was given by Jackson & Davies (1982). Site 2 which is also undisturbed is a small steep stream with a pool-riffle sequence draining mountainous forest country. The substrate consisted of cobbles and gravel, the flow was high, fast and turbid, the conductivity was 150 EC and water temperature was 10°C. It is possible that the specimen found at this site had been washed from areas of low-lying pasture during recent rains.

All new sites were characterised as being modified with all riparian vegetation removed, and sites 3 and 4 had also been channelized.

Site 3 is a shallow channel (1 m wide, 0.2 m deep) with a 0.8 m mud substrate and with water 20–30 mm deep draining from a spring in a pastured paddock into the Calder River. At the time of collection (17 October 1990) the channel had recently been excavated and little vegetation was present. Dissolved oxygen concentrations were 5.7 mg/L, pH was 7.0 and conductivity was 680 EC at 8.0°C. On 27 February 1991 the drain was heavily vegetated with a variety of native and introduced species of aquatic and pasture vegetation, the water was 20–30 mm deep, and the mud substrate was 200–400 mm thick.

Site 4 is a shallow drain (0.2–0.4 m deep) with a silt substrate leading from a spring in a cleared paddock into the Aire River. On 24 August 1990 most of the site consisted of a 2 m wide channel together with a larger 15 m × 20 m area, and was densely vegetated with aquatic species. Conductivity was 185 EC at 10°C. On 17 October 1990 dissolved oxygen concentration was 5.6 mg/L, pH was 6.7, and conductivity was 850 EC at 17°C. On 27 February 1991 there was 100 mm of mud and a little water up to 20 mm deep in cattle hoof prints in the channel. The larger area had shrunk to 3 m × 20 m with up to 100 mm of water and 300 mm of mud. Sections of the drain often become dry during summer but other sections always remain moist due to an underground spring (D. Denney pers. comm.).

Site 5 is a small billabong (60 m × 5 m × 0.8 m deep) about 30 m from the Aire River. No flow was apparent and the substrate was silt with dense aquatic vegetation. On 16 October 1990 the water was dark tannin in colour and had a dissolved oxygen concentration of 4.0 mg/L, pH of 6.4 and conductivity of 190 EC at 16.5°C. One specimen of *G. cleaveri* was collected from just inside a large log lying in the water. On 27 February 1991 the site was completely dry, a condition not unusual for this season (D. Denney pers. comm.).

All sites are at low altitudes (a maximum of 20 m above sea level) and close to the sea (a maximum of 8.5 km from the sea but only 3 km from brackish water). Except for site 2, all sites had no discernible flow and had mud or silt substrates and dense aquatic vegetation. Although Andrews (1976) considered that *G. cleaveri* tolerated brackish water, all our specimens were collected from fresh water. The drain leading from site 3, however, flowed into reaches of the Aire River which are known regularly to contain an estuarine salt-wedge under low flow conditions (J. Koehn pers. obs.).

The presence of *G. cleaveri* at these sites is consistent with its occurrence elsewhere in swamps, drains and semi-permanent waters. *G. cleaveri* was collected from stagnant pools in Tasmania (Andrews 1976) and from a drainage system usually dry in summer on Flinders Island (Green 1984). Fulton (1986) also recorded *G. cleaveri* from a dry section of the Esperance River in Tasmania. In New Zealand three species of mudfish, *Neochanna burrowsius*, *N. apoda* and *N. diversus*, have also been described as specialised to life in swamps, creeks and drains that tend to dry up in summer (Eldon 1968, 1978, 1979a, McDowall 1990).

Scott (1934) described *G. cleaveri* as one of the most specialised galaxiids in having adopted a mode of life suited to such habitats. Such adaptation and an association with low altitude, swampy habitats is likely to indicate a high degree of dependence on the presence of appropriate habitats. Collection of the species in Victoria from disjunct and highly modified areas containing introduced vegetation suggests that these populations may be remnants of a larger population that once existed when suitable habitats were more widespread.

BEHAVIOUR

We kept four *G. cleaveri* from site 3 in a glass aquarium (0.36 × 0.45 × 0.10 m) containing a silt

substrate and vegetation from the site. The behaviour and position of the fish were observed at intervals throughout each day for three weeks, and at 5 minute intervals for 1 hour during one night.

Generally the fish were inactive during the day, resting either on the substrate or amongst vegetation, and were difficult to locate because of their colour and cryptic habit. Individuals spent time resting either on the substrate wherever cover was available, or amongst dense weed just below the water surface. In both situations, several individuals shared the same cover and were in physical contact with each other. This behaviour is similar to that described by Eldon (1969) in *Neochanna apoda* which is also territorial and aggressive to other species in aquaria (Eldon 1968). Individuals of *G. cleaveri* exhibited no such aggressive behaviour to each other or to individuals of *Galaxias maculatus* or *G. truttaceus* which were placed into the aquaria at different times. At night *G. cleaveri* were more active, continually moving around open areas "browsing". At least two of the fish were in open areas at each observation. They immediately retreated into the vegetation when exposed to either white or red light but had always reappeared in the unvegetated areas by the next observation.

Our observations indicate that *G. cleaveri* is a nocturnal, cryptic species which often inhabits the aquatic vegetation rather than the substrate. Other species of galaxiids reported to be nocturnal are *Neochanna apoda* (Eldon 1968), *Galaxias brevipinnis* (Glova & Sagar 1989a), and *Galaxias vulgaris* Stokell (Glova & Sagar 1989b).

AESTIVATION

Scott (1934) gave details of the ability of *G. cleaveri* to aestivate, though under unnatural conditions. This ability has been noted by several other authors (Fletcher 1907, Hall 1901, Fulton 1986) though their descriptions mainly concern recovery of aestivating individuals. Fulton (1986) provided photographic evidence of *G. cleaveri* aestivating during mid-summer under a rock at least 10 m from free water.

McDowall & Pusey (1983) reported aestivation in *Lepidogalaxias salamandroides*, and aestivation of *Galaxiella pusilla* was suggested by McDowall & Frankenberg (1981). Humphries (1985) tested this suggestion by maintaining specimens of *G. pusilla* in an aquarium for 36 days whilst lowering water levels and maintain-

ing oxygen concentrations at less than 5 ppm. Fish survived on the surface of the mud and in a small hole for several days in the absence of surface water. McDowall (1990) presented evidence of the ability of the New Zealand mudfishes *Neochanna burrowsius* and *N. apoda* to survive dry periods, though both Eldon (1978) and Meredith (1985) concluded that these species do not exhibit true aestivation during which the individual becomes torpid and the normal rate of metabolism decreases.

We investigated whether burrowing and aestivation could be induced in *G. cleaveri* by placing two individuals (101 mm and 78 mm TL) into a glass aquarium (0.3 × 0.62 × 0.3 m) containing a substrate of soil and mud, a large flat rock at one end, dense aquatic vegetation in the middle, and a piece of log at the other end. The water level was lowered artificially, and heating and illumination were provided during the day by an incandescent globe. On day 10 some tunnelling in the middle section of the tank was observed, and one fish was seen lying near the water surface where it spasmodically gulped water and air. On day 14, when the water level had fallen to 10 mm above the substrate, one fish was resting in a vertical shaft in the mud with its head just protruding. On day 22 neither fish could be seen and no surface water remained, though water was present in the opening of the shaft. Later on the same day the heads of both fish were positioned in the shaft opening and their bodies were under the mud in horizontal tunnels. On day 25 a series of smaller openings were observed in a line directed away from the large shaft, presumably along the horizontal tunnels. On day 31 there was no water in the pit of the large shaft, the mud substrate had begun to dry, and one *G. cleaveri* had its head protruding from the tunnel into the shaft below the surface of the substrate. On day 32, after 5 days without any free water, the fish in the tunnels stopped moving. On day 42 when the substrate had dried to only 30 mm thick the two *G. cleaveri* were seen through cracks in the dry mud lying in the tunnels. The tank was then slowly rehydrated, and the fish recovered movement and emerged when the mud became soft. They both immediately fed on earthworms and showed no ill effects from surviving in stagnant water for 14 days and without surface water for another 14 days.

Whilst not physiologically confirming the ability of *G. cleaveri* to aestivate, our study shows that the species can survive periods without free surface water by burrowing into the substrate.

LIFECYCLE

Two male *G. cleaveri* collected at site 4 on 31 May 1990 were in a ripe spawning stage (Pollard 1972), whereas individuals collected on 24 August 1990 were all spent or undeveloped, indicating a winter spawning. These observations are consistent with those of Andrews (1976) who reported fully developed eggs in a specimen of *G. cleaveri* examined in Tasmania during May. After ageing whitebait returning to freshwater as approximately 2 months old, Fulton (1986) suggested that *G. cleaveri* spawn during mid-winter, and he believes (W. Fulton pers. comm.) that juvenile *G. cleaveri* return to fresh water during spring along with other galaxiids.

Cadwallader (1975) and Eldon (1979a) concluded that *Neochanna burrowsius* in New Zealand spawns during late winter and early spring in habitats frequented by adults. In contrast, Eldon (1979a) suggested that *N. apoda* spawns during most months of the year, especially when a drought breaks. Because Eldon (1971) found that in an aquarium *N. apoda* deposited eggs above the waterline, he speculated that in the wild the species deposits eggs out of the water amongst damp vegetation and detritus. The spawning location of *G. cleaveri* has not yet been found.

Present evidence indicates that *G. cleaveri* is unique amongst galaxiids in possessing the two characteristics of aestivation and diadromy.

THREATS AND CONSERVATION STATUS

General threats to freshwater native fish in Victoria have been described by Koehn & O'Connor (1990b) who considered habitat removal and alteration a prime reason for the decline of many species. The reliance of *G. cleaveri* on specific habitat would appear to make it susceptible to habitat changes, particularly the loss of wetland habitat.

The maintenance of fish habitats has been recognised as a key issue in management of the State's freshwater fish fauna (Koehn & O'Connor 1990c). Whilst up to one-third of the State's wetlands have been destroyed (DCE 1988), most of the assessments have related only to waterbirds; further assessments in relation to changes to fish habitats are necessary. Corrick (1981, 1982) and Corrick & Norman (1980) assessed coastal wetlands in southern Victoria and assigned them to the following categories.

1. Flooded river flats: land inundated for very short periods following rain or flooding.

2. Freshwater meadows: land with waterlogged soil for up to 3 months each year but where surface water is shallow and transient.
3. Shallow freshwater marshes: land with waterlogged soil throughout the year, and where surface water may be present for 6 to 9 months.
4. Deep freshwater marshes: land inundated to a depth of more than 1 m during years of average or above average rainfall.
5. Permanent open fresh water: water storages and natural lakes deeper than 1 m.
6. Semi-permanent saline wetlands.
7. Permanent saline wetlands.

From our knowledge of the habitats of adult *G. cleaveri*, shallow freshwater marshes (category 3) and deep freshwater marshes (category 4) appear to provide permanent areas of habitat. Flooded river flats and freshwater meadows may be used temporarily by the species during migration of whitebait or migration of adults to estuarine areas. Open fresh water (category 5) is unlikely to be used, particularly if lacking vegetation. There is no evidence to suggest that saline wetlands (categories 6 and 7) provide suitable habitats.

In a study of the Snowy River and Gippsland Lakes catchments, Corrick & Norman (1980) concluded that 25% of shallow and 34% of deep freshwater marshes have been lost. Within the Port Phillip Bay region, valuable wetlands lost include the Edithvale-Carrum-Seaford Swamps (Champion 1977, Donnelly et al. 1985) and the swamps of the lower Yarra and Maribyrnong Rivers (Castelnau 1872, excerpts from a diary kept by J. Flemings reprinted in Shillinglaw 1879, Kenyon 1934, and Ducker 1985). After studying wetlands between Port Phillip Bay and Mt Emu Creek in western Victoria, Corrick (1982) concluded that 79% of shallow and 66% of deep freshwater marshes had been lost since European settlement, an overall loss of 73% of potential *G. cleaveri* habitat. The most extensive habitat loss, however, is in South Gippsland where 95% of the natural freshwater wetland once present has been destroyed (Corrick 1981). South Gippsland also includes the largest areas of potential *G. cleaveri* habitat because it contains coastal-draining wetlands only within 40 km of the coast, unlike the other areas where wetlands extend as far as 150 km inland.

More than 23,000 ha of wetlands have been lost in South Gippsland, including Koo-Wee-Rup, Cardinia and Yallock Swamps, and swamps along the Powlett and Tarwin Rivers.

Corrick (1981) predicted further loss of wetland areas through drainage, clearing, cultivation and flood mitigation and irrigation works. His prediction appears fulfilled because calculations from recent studies of this area (Corrick unpubl. data) show an overall loss of 99% of potential *G. cleaveri* habitat (shallow freshwater marshes 94%, deep freshwater marshes 99%).

The loss of such large areas of habitat suitable for *G. cleaveri* must be the greatest threat to this species in Victoria in recent times and may account for its fragmented distribution. Similarly, Frankenberg (1974) stated that the range of *G. cleaveri* in Tasmania had undoubtedly been fragmented due to the draining and clearing of swamps.

In New Zealand populations of the three species of mudfish have declined drastically with the loss of habitat due to swamp drainage, development and agricultural practices (McDowall 1990). Whilst concern has been expressed for all three species, Skrzynski (1968) and Eldon (1979b) have questioned whether *Neochanna burrowsius* can survive, especially with continued agricultural modifications. Cadwallader (1975) suggested that preservation of habitat areas through the establishment of reserves should be instigated for this species. A population of *N. burrowsius* established in an artificial pond (Eldon 1988) survived for several years before dying out as a result of a prolonged drought (NZ MAF 1990).

Other threats to adult *G. cleaveri*, such as interspecific competition and predation by introduced trout, *Salmo trutta*, *Oncorhynchus mykiss* or redfin, *Perca fluviatilis*, are unlikely to be major, especially in swampy habitats with poor water quality unsuitable to these species. *G. cleaveri* whitebait may be subject to predation, however, whilst migrating upstream. Habitat disturbance and competition from other introduced species such as carp, *Cyprinus carpio*, goldfish, *Carassius auratus*, and tench, *Tinca tinca*, are possible but difficult to assess. Sedimentation is unlikely to affect *G. cleaveri* unless the habitat areas become completely filled.

Because *G. cleaveri* is restricted to a specialised aquatic habitat, climatic changes may have serious impacts, although the impact of the Greenhouse Effect is as difficult to predict as it is for other native species (Burchmore 1990). Lower winter rainfall may affect spawning and particularly access to the sea, and an increase in the tidal limit may alter available wetland habitat for mature *G. cleaveri*.

In a recent review of the conservation status of native fish in Victoria (Koehn & Morison 1990) *G. cleaveri* was listed as vulnerable, a category including "taxa not presently endangered but which are at risk by having small populations and/or by occupying restricted habitats susceptible to rapid environmental change and/or populations which are declining at a rate that would render them endangered in the near future". Although we have documented additional localities for *G. cleaveri*, our results reinforce the rarity of the species. The reductions in available freshwater wetlands and ongoing threats to such habitats justify the retention of *G. cleaveri* in the vulnerable category.

CONCLUSIONS

G. cleaveri is more widespread in Victoria than previously believed, occupying natural and modified habitats along lowland coastal areas, at least from Wilsons Promontory to the western Otways. There is a need for further surveys to determine the range of the species in swampy habitats within and outside of this area, particularly on French Island which contains remnant tea-tree swamp habitat that once existed throughout the Koo-Wee-Rup swamp area and the entire Western Port catchment. The discovery of *G. cleaveri* in this area would strengthen arguments that present populations are remnants of a once much larger, more uniformly distributed population. Collection of whitebait as they ascend coastal streams may also be a useful method of determining *G. cleaveri* distribution (Koehn & O'Connor 1990a).

The behaviour and habitat needs of this species are similar to those of the New Zealand mudfishes. The specific habitat needs of *G. cleaveri* make it particularly susceptible to habitat changes; therefore the massive reductions in suitable freshwater wetland habitats have undoubtedly been the greatest threat to the species. The management and conservation of such wetland areas are vital for the preservation of *G. cleaveri* in Victoria.

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FIRST RECORDS OF *MIRACYTHERE* HORNIBROOK, 1952 (CRUSTACEA, OSTRACODA) FROM THE TERTIARY OF AUSTRALIA

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NEIL, J. V., 1991:12:31. First records of *Miracythere* Hornibrook, 1952 (Crustacea, Ostracoda) from the Tertiary of Australia. *Proceedings of the Royal Society of Victoria* 103 (2): 87-92. ISSN 0035-9211.

A new species of the rare ostracode genus *Miracythere* Hornibrook, 1952, previously known only from New Zealand, is described from late Early or early Middle Miocene (Batesfordian) strata of the Muddy Creek Formation near Hamilton, southwestern Victoria. The new species is not formally named because the only complete adult valve amongst the limited material discovered has been lost. A specimen of another undescribed species possibly belonging to *Miracythere* is also figured from the Late Eocene of South Australia. The literature relating to this genus is reviewed, and the morphological parallels between *Miracythere* and some Palaeozoic genera are briefly discussed.

MIRACYTHERE is a rare and distinctive ostracode genus erected by Hornibrook (1952) for his new species *M. novaspecta* from dredgings off the northern tip of New Zealand. He indicated that the type species is widely distributed in New Zealand waters, though no locality data were given. No other species of the genus has been described, and the only other documented occurrence of *M. novaspecta* has been two valves recorded from the Otago Shelf by Swanson (1979a).

Hornibrook (1952, 1968) gave the stratigraphic range of *Miracythere* as Late Eocene (Runangan) to Recent and of *M. novaspecta* as Early Miocene (Hutchinsonian) to Recent, but he did not record any fossil occurrences. He has recently informed me (written communication 1985) that the Eocene occurrence cannot be confirmed, but that a specimen of *M. novaspecta* is known from the Wharekuri Greensand of Late Oligocene (Duntroonian) age, at a locality on the Waitaki River in the South Island now submerged by a hydroelectricity scheme reservoir. That occurrence, and a broken specimen (Fig. 1B) of *Miracythere* that I have recovered from the Tuketja Member of the Blanche Point Formation of South Australia (Late Eocene; Jenkins et al. 1982), predate the Victorian species described in the present paper. I have also picked a specimen of another undescribed species of *Miracythere* from a sample supplied by Dr B. Hayward from the Pleistocene (Castlecliffian Stage) Wanganui Series of New Zealand (Fig. 2C). No other occurrences of the genus are known at present.

SYSTEMATIC PALAEONTOLOGY

Family BYTHOCYTHERIDAE Sars, 1866

Remarks. Hornibrook (1952) placed *Miracythere* in the Bythocytherinae but noted that the hinge, with a posterior tooth in the left valve, is more complex than the characteristic bythocytherinid hinge. Schornikov (1981) regarded the genus as Bythocytherinae *incertae sedis*. Since I follow Hartmann & Puri (1974) in not recognising subfamilial groupings within the Bythocytheridae, the question of the placement of *Miracythere* at the subfamilial level does not arise. The hinge type as diagnosed by Hornibrook, and its variation in the Victorian species described here, fall within the range accepted as "normal" for bythocytherids.

Genus *Miracythere* Hornibrook, 1952

Type species. *Miracythere novaspecta* Hornibrook, 1952.

Diagnosis. See Hornibrook 1952: 61-62.

Remarks. A specimen from the Gulf of California and another of Cretaceous age from a deep sea drilling core in the Shatsky Rise, northwestern Pacific Ocean (DSDP 6-48.2) were tentatively assigned to *Miracythere* by Swain (1967; in Maddocks 1983). Both specimens differ from *M. novaspecta* in lacking a median sulcus, being longer, being caudate rather than subquadrate, and in having reticulate rather than smooth-surfaced valves. These differences

suggest that the specimens do not belong to *Miracythere*.

Miracythere sp. A

Figs 1A, C–D, 2A–B, 3A, C–F

Material. The specimens originally found consisted of one adult left valve (Figs 1A, D, 2A–B, 3A, C–F), one juvenile left valve, and fragments of two valves, all of which were lost in transit to the laboratory of the Geological Survey of Victoria. Subsequent repicking of the sample produced two broken juvenile valves, one left (NMV P123311, Fig. 1C) and one right (NMV P123312). The catalogue numbers refer to the invertebrate palaeontological collection of the Museum of Victoria, Melbourne.

Horizon and locality. Muddy Creek Formation, Clifton Bank, Muddy Creek near Hamilton, southwestern Victoria.

Age. All the specimens came from the oldest level at Clifton Bank (Sample 9), of late Early or early Middle Miocene (Batesfordian) age (N8 in the planktonic foraminiferal zones of Berggren et al. 1985; the revised correlation of magnetic anomalies by Berggren et al. has shifted ages 1.5 to 2.0 my younger in the Middle Miocene, so that the position of the Early–Middle Miocene boundary in relation to the Australian Bairnsdalian and Balcombian stages is open to debate.)

Dimensions. Adult LV: L = 0.65 mm; H = 0.38 mm; W = 0.23 mm (figured specimen, now lost). The repicked specimens NMV P123311 and P 123312 are too fragmentary to measure.

Description. Valve medium-sized in adult; subelliptical in outline, hyaline and thinly calcified. Surface smooth. Normal pore canals simple and widely scattered. Dorsal margin straight. Ventral margin straight to slightly sinuous, subparallel to dorsal margin except posteriorly. Anterior and posterior gently rounded in outline, former more so than latter. Anterodorsal and posterodorsal angles broadly and evenly rounded. Shallow, vertical median sulcus. Prominent hollow tubercle developed anterodorsally (Figs 1A, 3A), ornamented with three spines on dorsal edge. Valve inflated, with well-developed and sharply-defined flattened ventral zone; less marked flattening anteriorly and posteriorly. Inflation of valve greatest in posterior third. Marginal zone of valve and inflated area ornamented with flat spatulate spines (Fig. 3E) that vary in orientation, from normal to plane of valve dorsally, to parallel with that plane ventrally. Ends of spines trilobate, bilobate or pointed (Figs 3E, F). Spines absent along dorsal margin. Ventrally, spines separated from basal

plane of valve by slightly flanged rim. Approximately 30 spines in one row around inflated portion of carapace. Some spines probably missing through damage to valve. Spines 2 or 3 times more numerous on juvenile specimens than on adult. Ventral marginal zone of inflated area flat and normal to valve plane, forming broad basal platform 0.2 mm across (single valve).

Hinge-line marked in left valve by simple, smooth median bar with long, narrow grooves at anterodorsal and posterodorsal angles (Figs 2B, 3C, D). Muscle scar pattern consisting of 5 adductors in a compressed vertical row, with 2 small, subcircular frontal scars, one small ventral mandibular scar and 2 prominent dorsal scars (Fig. 2A). Inner margin moderately broad in anterior, narrow in posterior (Fig. 1D). Radial pore canals not detected. Line of concrescence deviates from inner margin; vestibule moderately broad anteriorly, narrow posteriorly. No eye tubercle. Sexual dimorphism not known.

Affinities. *Miracythere* sp. A differs from *M. novaspecta* (Figs 1E, 3B) in its more rounded ends and its spatulate rather than "peg-like" spines which occur in a single row marginal to the valve and the inflated area, rather than in 2 or 3 rows. The tubercle of the present species also carries spines rather than the pustules found on *M. novaspecta* (Fig. 3B). Additionally, there is no tooth in the hinge elements of the left valve. *Miracythere* sp. A resembles the type species in the median vertical sulcus, the ornamentation of spines, the muscle scar pattern and the shape and appearance of the carapace in lateral view. These features clearly establish the species as belonging to *Miracythere*.

Remarks. *Miracythere* sp. A is more closely allied morphologically to the Pleistocene specimen from New Zealand (Fig. 2C) than it is to *M. novaspecta* (Fig. 1E), having a similar arrangement of spines, a lophodont hinge structure and a similar subrounded quadrate shape. However, the Pleistocene specimen does not have a clearly differentiated, inflated inner lateral section of the valve as found in *Miracythere* sp. A. The fragmentary valve from the Late Eocene of the Blanche Point Formation, South Australia (Fig. 1B) may be conspecific with *Miracythere* sp. A.

The dimensions of the lost adult specimen of *Miracythere* sp. A were the same as those of the holotype *M. novaspecta*, allowing for the fact that the former specimen was a single valve whereas the latter is a carapace. It was not possible to determine whether this adult valve be-

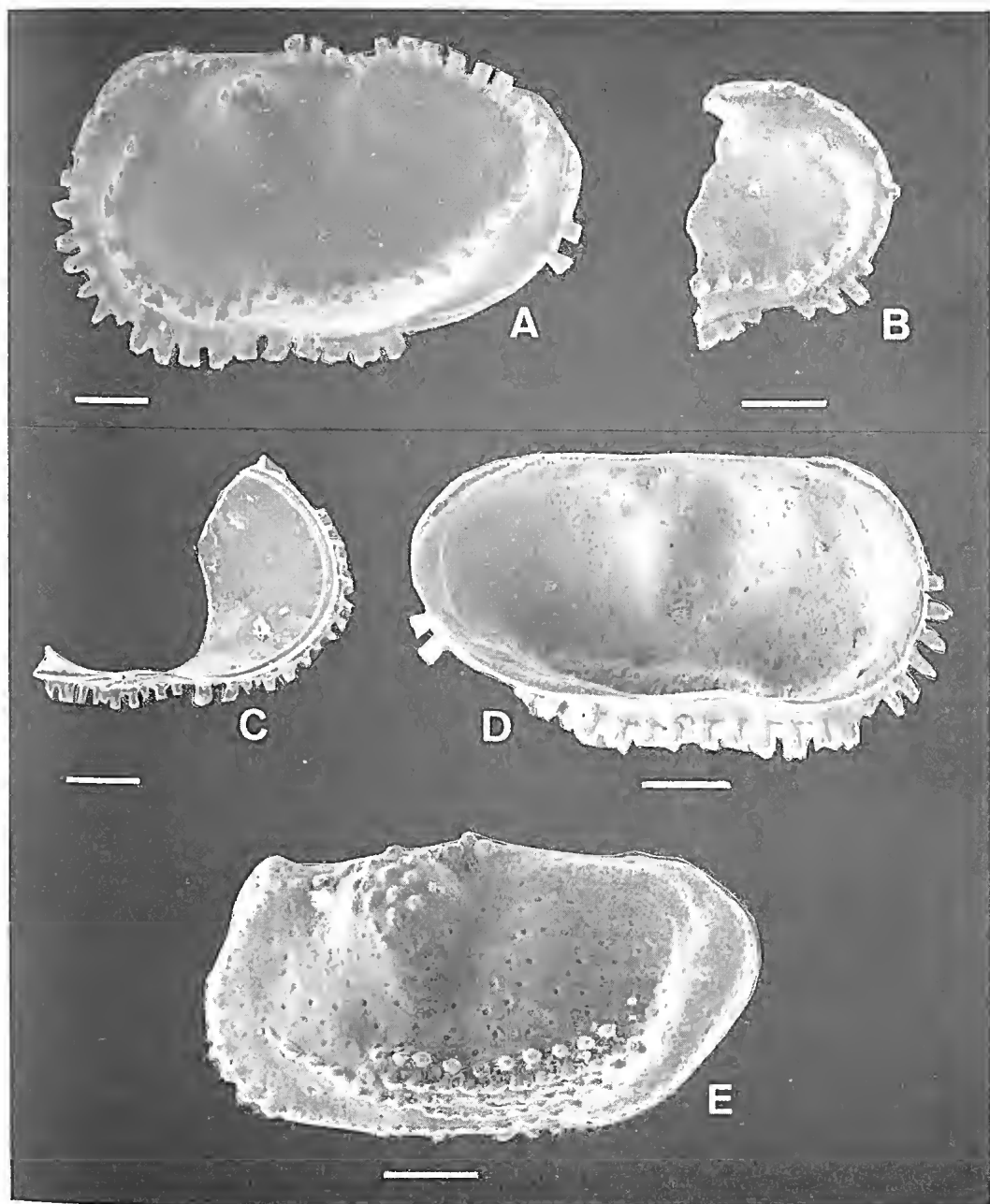


Fig. 1. A, C, D, *Miracythere* sp. A. Muddy Creek Marl (early Middle Miocene), Clifton Bank, Muddy Creek, southwestern Victoria. A, D, LV exterior and interior (specimen lost). C, LV interior (fragmentary juvenile), NMV P123311. B, ?*Miracythere* sp., LV exterior (fragment), Tuketja Member, Blanche Point Formation (Late Eocene), Port Willunga, South Australia. E. *Miracythere novaspecta* Hornibrook, 1952, LV exterior, New Zealand Geological Survey fossil locality F201012, Station 18 of Hornibrook (1952), off Big King Island at 98 fathoms. Scale bars = 0.1 mm.

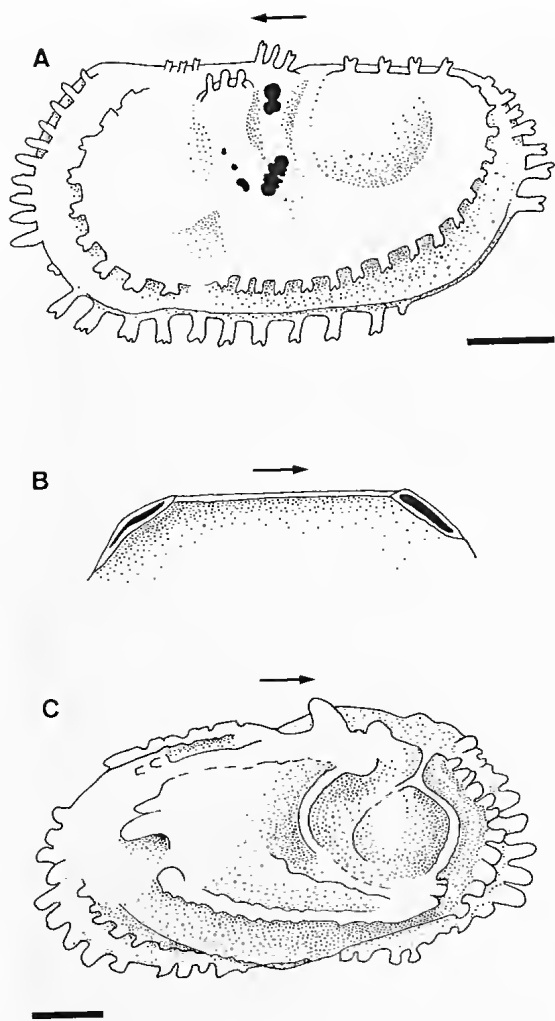


Fig. 2. A–B, *Miracythere* sp. A. A, drawing of LV interior showing muscle scars. B, drawing of LV hinge line (not to scale). C, ?*Miracythere* sp., drawing of RV exterior, from Wanganui Series (Castlecliffian, Pleistocene), Wanganui, New Zealand. Scale bars = 0.1 mm.

longed to a male or to a female. The juvenile specimen (now lost) was close to the adult in lateral dimensions but was much less inflated, suggesting that in the final growth stage or stages there was little change in length or height but an increase in width. However, Swanson (1979a) figured a specimen of *M. novaspecta* that he considered to be a juvenile, though its length and height are virtually the same as those of the holotype and its width is actually greater.

The hinge structure of *Miracythere* sp. A is closer to the typical bythocytherid form than to that of the type species. In the latter, the left valve anterior groove or socket of the hinge elements extends above the dorsal line established by the median bar, and marks the anterodorsal angle in pronounced fashion (Fig. 3D). *Miracythere* sp. A has a narrow anterior groove which continues the line of the median bar, paralleling the broadly rounded anterodorsal angle (Fig. 3C). The left valve posterior hinge element of *M. novaspecta* consists of a narrow tooth below, with a groove or socket above at the posterodorsal angle. *Miracythere* sp. A has a groove (in a more elongate form), no tooth and a less marked posterodorsal angle (Fig. 3C). The Victorian and Late Eocene South Australian specimens have a lophodont hinge structure. Given that the variation in hinge structure is a relatively minor one, the specimens should be retained in *Miracythere*.

As with the genera *Puncia* and *Manawa* erected by Hornibrook (1949), morphological parallels may be drawn between *Miracythere* and some Palaeozoic genera. Ruggieri & Siveter (1975) figured a species of *Kelletina*, *K. carnica*, in which there is ventrally a broad flat platform or flange with marginal spines, some of which are linked to form a perforated ridge. *Kelletina carnica* also has a lophodont hinge structure very similar to that of *Miracythere* sp. A. The right valve of *K. carnica* has a simple tooth at each of the anterodorsal and posterodorsal angles to match the grooves in the left valve. The unknown right valve of *Miracythere* sp. A is likely also to have such teeth. A further similarity with Palaeozoic genera lies in the muscle scar pattern, which in both *Miracythere* and *Promanawa* McKenzie & Neil, 1983 includes prominent dorsal antennal/mandibular scars.

Morphological similarities with Palaeozoic forms gave rise to speculation about the phylogeny of the Punciidae by Hornibrook (1949, 1963), even though at that time no Mesozoic representatives of the family were known. Herrig (1988), however, has recently discovered species of all three punciid genera, *Puncia*, *Manawa* and *Promanawa*, in silicified chalky limestone of late Maastrichtian age. Swanson (1991) made an intensive study of the soft part anatomy of punciids, as well as their carapace morphology, and concluded that "On the basis of a detailed comparison of a number of key carapace characters ... punciid ostracods are the only living representatives of the predominantly

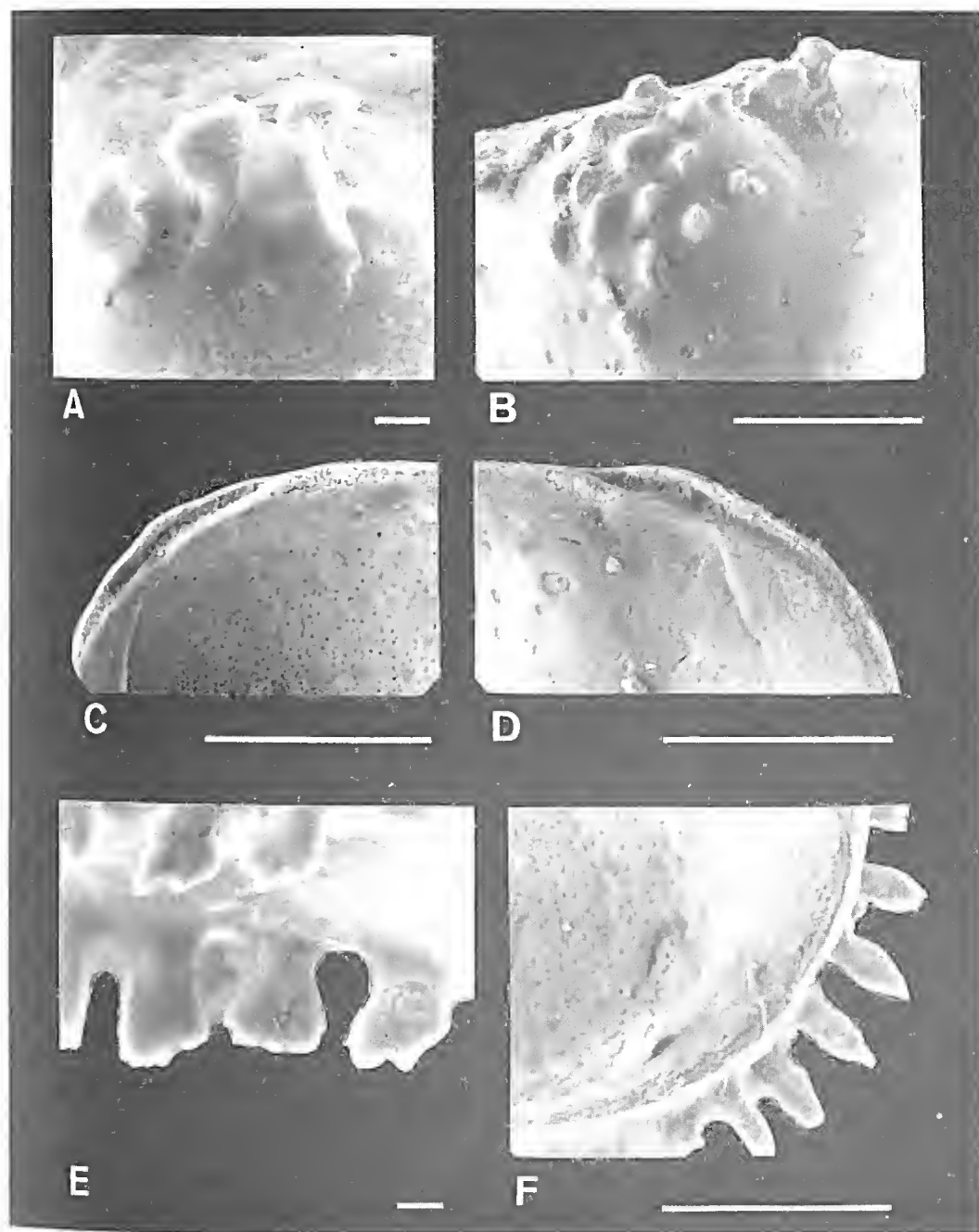


Fig 3. A-C-F, *Miracythere* sp. A, A, spines on tubercle. C, posterior hinge line. D, anterior hinge line. E, spatulate spines on ventral margin. F, pointed spines on anteroventral margin. B, *Miracythere novaspecta* Hornibrook, 1952, pustules on tubercle. Scale bars = 0.01 mm in A and E, 0.1 mm in remainder.

Palaeozoic Kirkbyacea." Morphological similarities between *Miracythere* and Palaeozoic forms are less suggestive of phylogenetic links, since the homologies are shared with a number of Recent genera. Since *Miracythere* occurs only in Recent and Tertiary sediments, as was believed to be the case for the puncliids (Swanson, 1979b, 1985), the absence of Mesozoic records of it or of *Kelletina* at present nullifies any hypothetical phylogeny of *Miracythere* linking it with the latter genus. The discovery of *Miracythere* in Late Eocene sediments in a form possibly conspecific with *Miracythere* sp. A gives an age range in southeastern Australia greater than that for *M. novaspecta* in New Zealand. This suggests that the Mesozoic *Miracythere* gap might also be filled in the course of further intensive collecting, so that the possibility of an evolutionary origin in a Palaeozoic kirkbyacean is not ruled out. A more plausible view, however, is that the basic morphology of *Miracythere* is the result of convergent evolution of bythocytherids. The occurrence of ?*Miracythere* sp. in the Pleistocene of New Zealand in a form which reflects some of the characteristics of *Miracythere* sp. A whilst differing markedly from *M. novaspecta* suggests that a plexus of species of this genus may eventually be discovered.

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ECOLOGY OF TWO ASCLEPIAD LIANES IN SEMI-ARID VICTORIA

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Marsdenia australis and *Rhyncharrhena linearis* (Asclepiadaceae) are lianes of the “thin wiry” type. In Victoria they are found in semi-arid woodlands, secondary shrublands and mallee communities. Both can sucker profusely from the roots to form large clones but only *Marsdenia* has tuberous roots. Both species have a pair of foliar glands per leaf adaxially at the leaf base.

Fresh seed of both species has high germinability and most germinated in a few days, especially at 25°C. Germinability of *Marsdenia* seed declines with time and is zero at 14 yr. At 18 weeks old, *Marsdenia* seedlings have higher dry weights than those of *Rhyncharrhena* due to their well-developed tuberous root systems.

Although both species flower annually, there is regular November–December *Marsdenia* flowering, even in very dry conditions, whereas only a few *Rhyncharrhena* flowered after heavy rain within the January–April period during our study. Fruit set was low for both species, especially *Rhyncharrhena*. Both species showed some increase in shoot length from February to September; this is most rapid when rain falls during warm weather. During drought, *Rhyncharrhena* plants rapidly lost leaves while *Marsdenia* plants did not. Tuberous roots may allow *Marsdenia* to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Both species are now vulnerable in Victoria. It is thought that the main threat is grazing by stock and rabbits. Fruiting has only been seen in plants which are climbing above 0.5 m in shrubs or trees; deliberate introduction of long-lived woody plants is needed to ensure seed production of *Marsdenia* and *Rhyncharrhena* in some grazing enclosures.

THE ASCLEPIADACEAE is a predominantly pan-tropical family of about 2000 species, mostly of woody climbers, perennial herbs and shrubs. The 60-odd Australian species occur mainly in the east and north, especially in rainforest, but a few species are widespread in semi-arid to arid areas and reach temperate latitudes (Williams 1984). Of the 12 or so important dicotyledonous liane families, Asclepiadaceae and Convolvulaceae (see below) are two which especially spread beyond rainforests into seasonally dry areas, both in Australia and elsewhere (Forster 1988, Hegarty 1989, Vahrmeijer 1981).

Lianes show decreasing robustness with decreasing annual rainfall; those dealt with here belong to the most slender of Webb's (1978) liane categories, being normally present as the “thin wiry” type (stem diameters less than 10 mm). In semi-arid north-western Victoria, there are seven native species which could be considered under this heading: *Marsdenia australis* and *Rhyncharrhena linearis* (Asclepiadaceae), *Jasminum didymum* ssp. *lineare* (Oleaceae), *Clematis microphylla* (Ranunculaceae) and

Convolvulus crispifolius, *C. erubescens* and *C. remotus* (Convolvulaceae). Species nomenclature follows Ross (1990) except that the name *Marsdenia australis* (R. Br.) Druce has been preferred to *Leichardtia australis* R. Br. following recent revisionary studies suggesting that *Leichardtia* is a synonym of *Marsdenia* (P. I. Forster personal communication). Inclusion of the *Convolvulus* spp. on the above list may be contentious as similar *Convolvulus* species are treated by some authors as herbaceous, not woody, climbers (Pate & Dixon 1982, Keeley & Keeley 1988).

Of Australian asclepiads, only a small number of species from *Cynanchum*, *Marsdenia*, *Rhyncharrhena* and *Sarcostemma* occur in semi-arid to arid regions. They show various features thought to be xeromorphic, like leaflessness and succulence (*Sarcostemma*) or reduced leaves (e.g. *Rhyncharrhena*) (Lapinuro 1976). The only such species occurring in Victoria, to be dealt with in detail below, are *Marsdenia australis* and *Rhyncharrhena linearis*. Other than these, the only native asclepiads in Victoria are



Fig. 1. Fruiting *Marsdenia australis* growing on *Dodonaea viscosa* at site 3 in March 1991.



Fig. 2. Fruiting *Rhyncharrhena linearis* growing on *Dodonaea viscosa* at site 1 in March 1991.

servation status rated as vulnerable Victoria-wide (Gullan, Cheal & Walsh 1990) so that data are needed as a basis for their management, and (2) that both were important aboriginal foods (Latz 1982) and *Marsdenia* in particular may be worth cultivating for its palatable fruits and its use as an indoor plant (Cherikoff & Isaacs no date, V. Cherikoff personal communication).

DISTRIBUTION AND HABITAT

Both species occur in inland parts of all mainland states of Australia including Queensland (Cunningham et al. 1981, Queensland Herbarium unpublished). There are records of both from at least as far north as 20°S, about the latitude of Tennant Creek (P. Latz personal communication) to as far south as 35°S near Walpeup in northwestern Victoria (this study).

Mean annual rainfall for both species can range from below 150 mm in the Great Victoria Desert (Greenslade, Joseph & Barley 1986) to above 400 mm in central New South Wales (Wilson 1980, Royal Botanic Gardens Sydney 1989). Seasonal rainfall distribution shows a slight May to October peak in Victoria (Badawy 1982) but changes to a summer maximum which becomes progressively more marked northwards (Slatyer 1962).

The whole area experiences hot summers and mild winters; mean temperatures increase steadily northwards. While frosts are very rare to absent north of 21°30', mean annual frost frequency ranges from 7 to 32 in the area from Alice Springs to northwestern Victoria without correlating closely with latitude (Slatyer 1962, Australian Bureau of Meteorology unpublished data). Mean length of frost season is more

two species of *Marsdenia* and one of *Tylophora* in the rainforests and adjacent tall open-forests of East Gippsland 600 km to the south-east.

The aim of this paper is to provide an introduction to the ecology of two asclepiads of arid and semi-arid areas, *Marsdenia australis* (Fig. 1) and *Rhyncharrhena linearis* (Fig. 2), at the temperate, southern limit of their range in Australia. *Rhyncharrhena* is one of only four asclepiad genera endemic to Australia, while *Marsdenia* is one of the most widespread genera, extending through parts of Asia, Africa and America. It is assumed that both *M. australis* and *R. linearis* were derived from northern Australian rainforest taxa in response to increasing aridity (Beadle 1981).

The work, nearly all in Victoria, is based on sporadic field observations from 1981 to 1989 and intensive work from January to December 1990. For brevity, the species will be referred to simply by their generic names. Two reasons for the project are (1) that both species have a con-

strongly related to latitude, reaching a maximum of 109 days in the south of the area in northwestern Victoria (Australian Division of National Mapping 1986, Badawy 1982). Given the recent emphasis on absolute minimum temperature in defining distribution limits (Woodward 1987, Booth 1990), such values range from 4.5°C at Tennant Creek, -7.5°C at Alice Springs, -2.8°C at Broken Hill, -4.0°C at Mildura, -5.8°C at Ouyen and -2.0°C at Walpeup (Australian Bureau of Meteorology unpublished screen temperatures).

Within the area studied in detail, northwestern Victoria, mean annual rainfall increases from 250 mm in the north (Neds Corner) to 343 mm in the south (Walpeup). Temperatures decrease and frost season increases at the same time; the areas south of about 35°S lacking *Marsdenia* and *Rhyncharrhena* are both wetter and colder than those areas supporting them (Badawy 1982). As growth of both species occurs especially in summer, decreased summer rainfall could possibly limit their distribution. However, there is no such decrease going from the north to the south of their Victorian range; some factor related to declining temperatures seems more likely to set their southern limits.

There is no clear evidence that the two species differ in their climatic tolerances.

A survey in 1985-6 of 1,300 20 m × 20 m quadrats in predominantly native vegetation in northwestern Victoria produced four records of *Marsdenia* and eight of *Rhyncharrhena* (Cheal & Parkes 1989 and personal communication), so these are not common species.

The Victorian distribution maps show 23 *Marsdenia* minor grid records and 15 of *Rhyncharrhena* (Fig. 3), partly reflecting the view that *Rhyncharrhena* is much the rarer of the two, e.g. in Victoria (J. N. Macfarlane personal communication) and around Broken Hill (Morris 1975).

In central Australia, most *Rhyncharrhena* plants are found in *Acacia aneura* communities, while *Marsdenia* occurs in most habitats (P. K. Latz 1982 and personal communication). However, in New South Wales both species occur in a wide range of communities, including those dominated by *Acacia aneura*, *Casuarina pauper*, *Eucalyptus intertexta* and various mallee species of eucalypt ("mallee") (Cunningham et al. 1981). In Victoria, the two asclepiads have very similar habitat ranges, both occupying relatively fertile sandy loams to clay loams carrying (1)

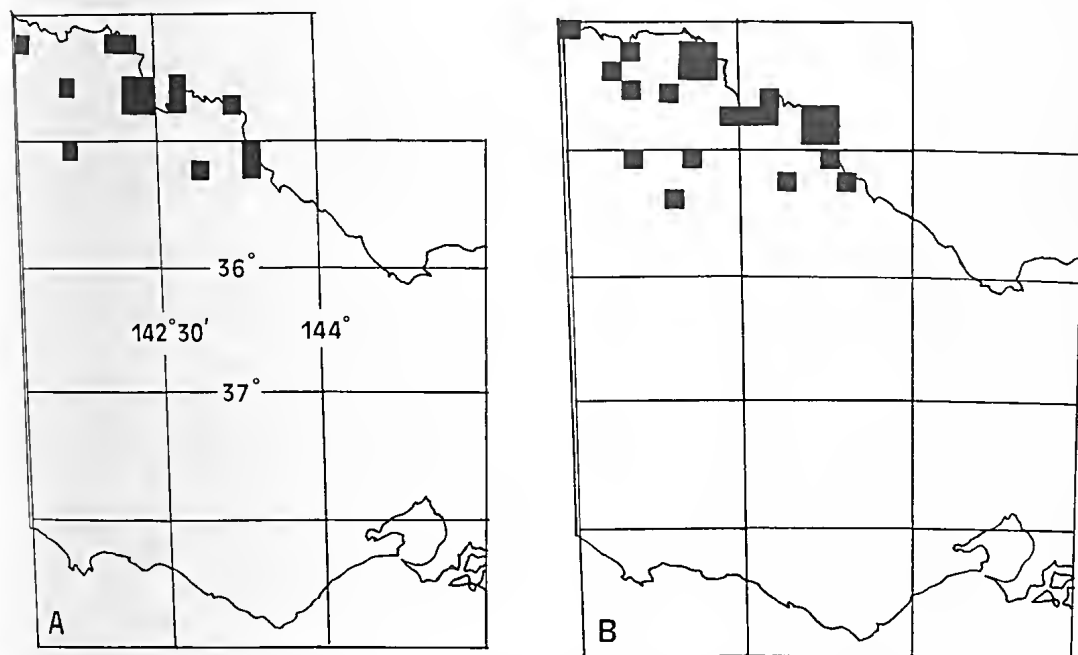


Fig. 3. Victorian distribution of (A) *Rhyncharrhena linearis* and (B) *Marsdenia australis* based on presence or absence within 10° latitude × 10° longitude grid squares for post-1950 records. All records from the Flora Survey and Management Group, Department of Conservation and Environment, with the addition of A31 and F29 for *M. australis*.

Site	Location ¹ /management	Mean annual rainfall ² (mm)	Area ⁴	Topsoil texture	Plant community	No. of shoots seen in 1990 adults/suckers	
						M	R
1	Department of Agriculture land, Campbell Avenue, Red Cliffs	285	8 ha	Sandy loam	<i>Cassia nemophila</i> - <i>Dodonaea viscosa</i> low shrubland ³	22/20	39/70
2	Red Cliffs Scenic Reserve	285	21 ha	Sandy loam	<i>Cassia nemophila</i> - <i>Maireana pyramidata</i> low shrubland ³	1/20	10/20
3	Red Cliffs Primary School Conservation Area	285	2 ha	Sandy loam	<i>Casuarina pauper</i> - <i>Callitris preissii</i> low woodland	9/15	3/10
4	Hattah-Kulkyne National Park	305	M 800 m ² R 225 m ²	Sandy loam	<i>Eucalyptus socialis</i> tall shrubland	1/10	1/100
5	Walpeup Flora & Fauna Reserve	343	50 m ²	Sandy clay loam	<i>Eucalyptus dumosa</i> open scrub	13/20	None
6	Pink Lakes State Park	312	M 1156 m ² R 1 ha	Sandy loam	M - Semi-cleared <i>Callitris preissii</i> low woodland R - Semi-cleared <i>E. socialis</i> tall shrubland	2/25	0/22

Table 1. Characteristics of Victorian *Marsdenia* and *Rhynchospora* sites examined in detail. ¹ See Appendix 1 for details. ² Using values from the Red Cliffs, Hattah, Walpeup and Underbool stations. ³ Secondary shrublands following clearance of woodlands like those at site 3. ⁴ M = *Marsdenia*, R = *Rhynchospora*.

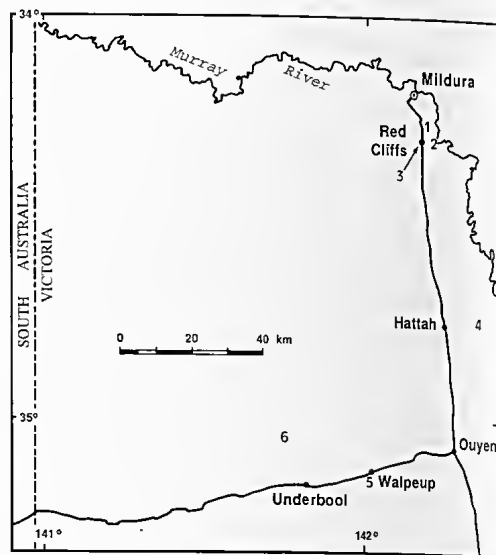


Fig. 4. Location of the study sites in north-western Victoria.

woodlands of *Casuarina pauper* and/or *Callitris preissii*, (2) various mallee communities or (3) various secondary shrublands following disturbance of (1) or (2) (see Table 1). They appear to be absent from the relatively infertile deep sands and from floodplains.

Sites for detailed study (Fig. 4) were chosen to encompass a range of mean annual rainfalls (Table 1, Appendix 1) and to include the largest populations known to us (sites 1, 3 and 5), as well as populations exclosed against grazing mammals in conservation reserves (sites 4 and 6).

MORPHOLOGY

Seed and seedling morphology

Marsdenia seeds are glabrous, dull, mid-to dark brown, flattened, finely winged, pyriform to ovate and comose at the narrower, germinating end. Germination is epigeal, the radicle emerging a minimum of two days from imbibition. Many short, fine root hairs develop as the radicle elongates (Fig. 5). The testa usually falls away in one piece. Sometimes it fails to fall off and dries, in which case it must be removed to allow seedling development as is the case in some other asclepiads (Harp 1987). The cotyledons are flat, petiolate and elliptical to obovate (Fig. 5). Tri-cotyledony occurs occasionally.

At 18 weeks, all seedlings have a tuberous taproot typically 10 mm in diameter with fine

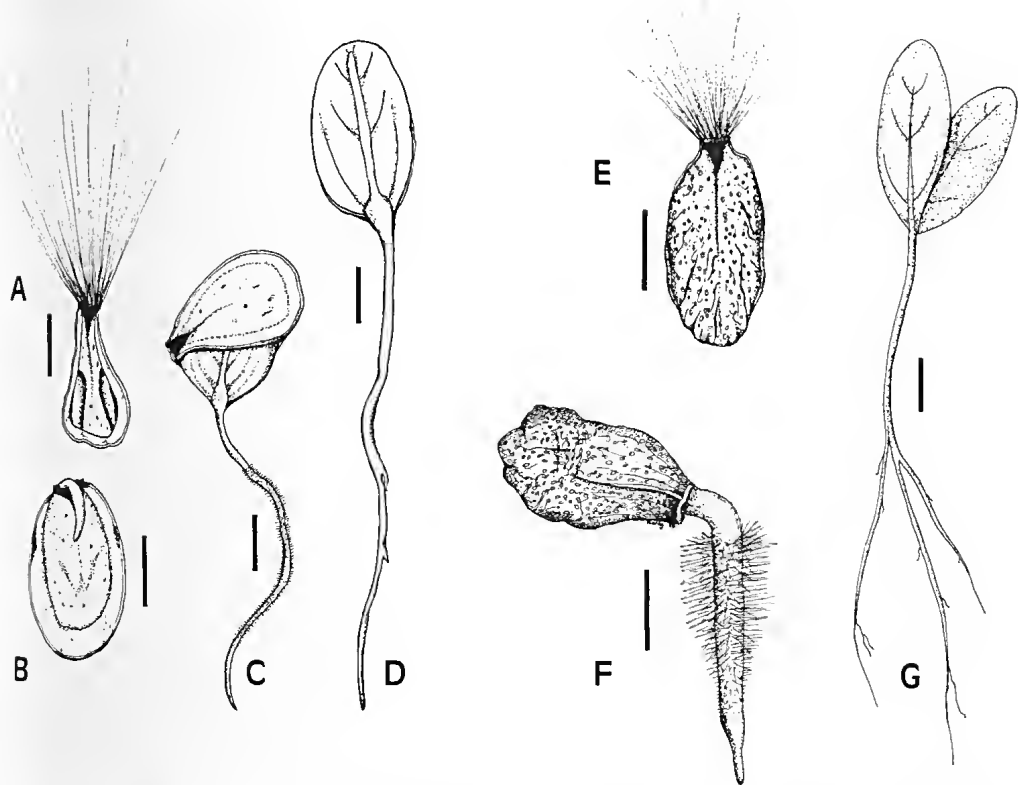


Fig. 5. Seeds and young seedlings of *Marsdenia australis* (A-D) and *Rhyncharrhena linearis* (E-G). A, E, dry seeds with comas. B, seed with radicle 2 days after sowing. C, F, seedlings 7 days after sowing showing root hairs. D, G, seedlings 12 days after sowing. Scale bars = 3 mm.

secondary roots (Fig. 6A) when the shoots are 440 mm tall.

On exceeding about 150 mm in height, the stem is unable to support the weight of the expanding leaves and bows over to become nearly horizontal; lateral shoots then develop from lower nodes. At this stage, the distal part of shoots can begin to revolve dextrorsely and to twine around any support encountered. Without support, the stem may bow almost to the ground and twine up about itself.

Rhyncharrhena seeds are rugulose, dull brown, flattened and elliptical to oblong. Germination and young seedling morphology are as for *Marsdenia* except for longer, denser root hairs and narrow-elliptical cotyledons (Fig. 5). No problem with persistent testas was found.

At 18 weeks, a root system lacking tubers is present (Fig. 6B); stem growth is similar to *Marsdenia*. There is no obvious ontogenetic change in leaf shape in either species.

Adult morphology

Shoots. Both species have opposite leaves lighter green and with denser stomata on the abaxial than on the adaxial surface. The stomata are modified rubiaceous type (Metcalf & Chalk 1957).

Stem diameter was typically 5–7 mm and up to 10 mm in *Marsdenia*, but only 3 to 5 mm in *Rhyncharrhena*. When no support is found by circumnating stems of either species, the stems can twine around themselves. In *Marsdenia* this can result in tightly plaited ropes up to 6 m long (Fig. 7); similar stems occur in the asclepiad *Araujia sericofera* (Menninger 1970).

Like most Australian asclepiads, *Marsdenia* and *Rhyncharrhena* are apical stem twiners, a type of behaviour said to be seldom effective in climbing trees of over 100 mm diameter at breast height (Hegarty & Clifford 1984). In this study, we found them twining up a range of

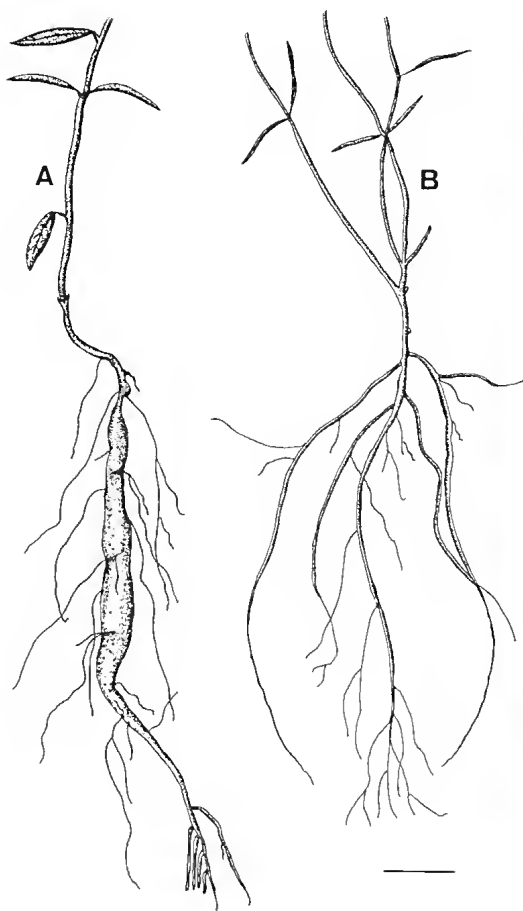


Fig. 6. Eighteen-week-old seedlings of (A) *Marsdenia australis*, showing tuberous taproot and (B) *Rhyncharrhena linearis* with non-tuberous roots. Scale = 20 mm.

shrubs and mallee eucalypts, with *Marsdenia* twining up eucalypt trunks of up to 90 mm diameter and to heights of at least 4 m. Where *Marsdenia* and *Rhyncharrhena* occurred in *Callitris-Casuarina* woodlands, we found them on shrubs but not on the trees. While there are records from large trees (e.g. photograph of *Rhyncharrhena* on *Callitris*, Victorian reference set, National Herbarium of Victoria), it may be that such trees were climbed many years previously when they had thinner stems.

Internode lengths were shorter for unsupported lianes than supported ones and were generally shorter for *Marsdenia* than for *Rhyncharrhena*. It was common to find small, unsupported shoots scattered in the vicinity of large, supported plants in both species.



Fig. 7. *Marsdenia australis*. A plait of five stems 35 mm in diameter at site 5; the plant extends from the soil surface to the crown of a mallee species of *Eucalyptus* (stem visible in background).

Roots and perennation. Parts of site 1 were excavated on 26–27 June 1990 to determine whether small, unsupported shoots were suckers or seedlings, and simultaneously to describe root systems.

Excavation of one adult *Marsdenia* plant and ten small shoots in an area of 2×1.5 m showed that all ten were suckers. Tissue sections showed that these arose from lateral roots. The suckers were from roots at depths of 100 mm to more than 500 mm below the surface and with diameters of 5 to 18 mm (Fig. 8A–C). They can occur more than 2 m from the parent plant.

Marsdenia has perennial tuberous roots, both laterals and tap-roots, the laterals up to 0.5 m long and 25 mm in diameter (Fig. 8A–C) and thus appreciably larger than those recorded in this species by Pate & Dixon (1982). The tuberous roots contain many large starch grains up to 10 μ m in diameter; the stems have fewer, smaller grains (2.5 μ m diameter). Copious branching leads to a complex system of tuberous

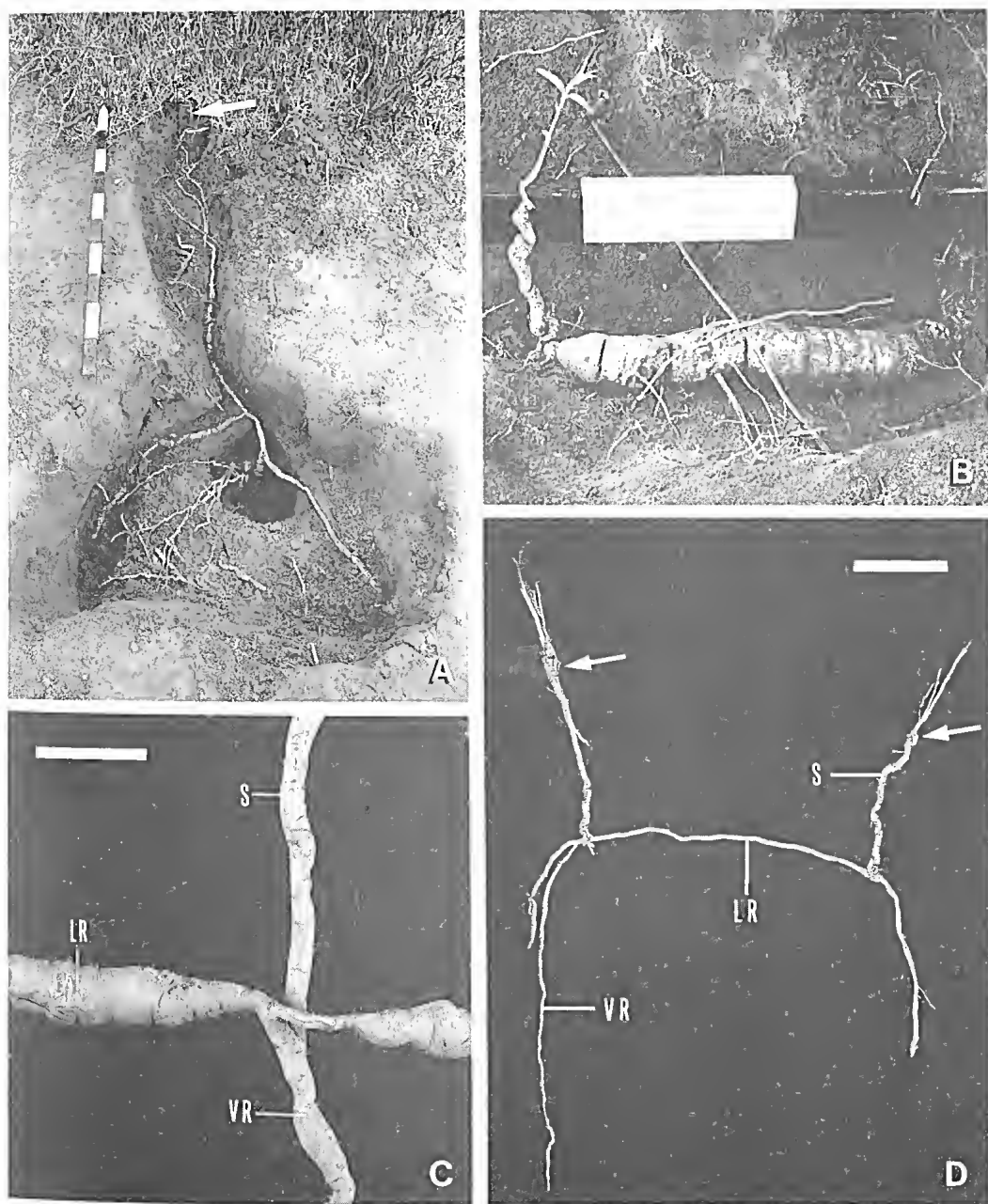


Fig. 8. A, partly-excavated root system of *Marsdenia australis* at site 1, showing tuberous horizontal and vertical roots. Arrow shows stem of adult plant. Scale divisions = 100 mm. B, part of *Marsdenia australis* plant at site 5, showing sucker shoot and tuberous root of 18 mm diameter. Scale divisions = 100 mm. C, part of *Marsdenia australis* plant at site 1 showing stem of sucker shoot (S), vertical root (VR) and tuberous root (LR) about 200 mm below soil surface. Scale = 30 mm. D, part of *Rhyncharrhena linearis* plant at site 1 showing two sucker shoots, stem (S), lateral root (LR), level of soil surface (arrow) and vertical root (VR). Scale = 50 mm.

roots in a number of layered, horizontal planes (Fig. 8A). Lateral tuberous roots were seen from 100 to 500 mm below the soil surface; vertical tuberous roots continued beyond 750 mm.

Tuberous roots are common in a number of liane families including the Asclepiadaceae, especially in species from seasonally dry areas rather than those from undisturbed evergreen rainforest (Hegarty 1989, Janzen 1975). Asclepiad examples include various African species of the succulent genus *Ceropegia* (Jacobsen 1960) and the Australian *Marsdenia flavescens*, *M. leptophylla* and *M. viridiflora* (Williams 1984).

Excavation of three small *Rhyncharrhena* shoots in an area of 500 × 200 mm showed them to be suckers, again from lateral roots (proved by tissue sections). Unlike *Marsdenia*, *Rhyncharrhena* roots are thin (diameter rarely greater than 5 mm) and non-tuberous, the laterals are not found deeper than about 200 mm and there is little branching (Fig. 8D). Starch grains are absent from the roots but present in the stems as before. Lines of sucker shoots strongly suggest that lateral roots can extend more than 15 m from parent plants (Fig. 9).

Root suckering, recorded here in *Marsdenia* and *Rhyncharrhena*, is known in other asclepiads, e.g. in *Morrenia odorata* (Tucker & Phillips 1974) and *Asclepias syriaca* (Bhowmik & Bandeen 1976) which can form clones of several thousand stems (Wilbur 1976). Such suckering may be "the most conspicuous form of

asexual multiplication" in tropical perennials and may, for all we know, produce very large individual plants of great longevity, each spread over many hectares (Janzen 1975). Such suckering may allow some liane individuals, including *Marsdenia laxiflora*, to persist more or less indefinitely in the absence of regeneration from seed (Penalosa 1984). Other aspects of suckering are dealt with later.

Without data on root depth limits and location of soil moisture reserves, we are unable to classify *Marsdenia* and *Rhyncharrhena* root systems into types. Clearly both have extensive lateral roots. *Marsdenia* roots extend beyond 750 mm deep and Pate & Dixon (1982) treat the species as deep-rooted, but further data are needed.

ANATOMY

Methods

Seedling tissue 18 wk old was fixed in 5% glutaraldehyde in phosphate buffer, dehydrated in a graded ethanol series and then infiltrated with LR White resin ('BioRad' Microscience Division, Hemel Hempstead) over 72 hr and polymerized at 65°C overnight. Thick sections were obtained using an American Optical Corp. Model 860 sledge microtome and stained with 1% safranin (aqueous).



Fig. 9. *Rhyncharrhena linearis* sucker shoots marked with flags at site 4. Mature plant from which the suckers are probably derived is approximately 10 m to the left of the photo inside the fenced plot.

Stem

The stems of *Marsdenia* and *Rhyncharrhena* have a continuous vascular cylinder traversed by narrow rays (Fig. 10) as in many other asclepiads (Metcalf & Chalk 1957). Both species have simple uniseriate hairs (Fig. 10A) and many druses attached to the wall of cortical cells (Fig. 10B). The cells of the hypodermis look very similar to those of the epidermis in both species.

Phloem occurs as small strands internal to the primary xylem (Fig. 10) in both species; such intraxylary phloem is universal in the family (Metcalf & Chalk 1957). Some vessel elements have larger diameter in *Rhyncharrhena* than in *Marsdenia* (Fig. 10). Both species have thick-walled fibres adjacent to the external phloem. In both, broken cells indicate the natural disintegration of the central pith to produce a lysigenous cavity (Fig. 10).

While laticifers are thought to occur in the shoots of all asclepiads (Metcalf & Chalk 1957), they can be difficult to distinguish (Metcalf 1966) and we were unable to identify any with certainty. Cut stems exude milky latex in *Marsdenia* as in most asclepiads, but not in *Rhyncharrhena* which we assume has watery latex as seems to occur in *Asclepias tuberosa* (Wilbur 1976), *Ceropegia cumingiana* (Bruyns & Forster 1989) and some other asclepiads (Williams 1984).

Foliar glands

A number of plant species including asclepiads have foliar glands or squamellae adaxially at or near the leaf base (Ramayya & Bahadur 1968). As their nature in asclepiads is almost unknown, they were examined in *Marsdenia* and *Rhyncharrhena*.

Both *Marsdenia* and *Rhyncharrhena* have a pair of glands per leaf adaxially at the leaf base (Figs 11, 12). The glands are up to 0.3 mm long and exude copious amounts of a sticky, transparent substance through a large pore in the centre of the gland head (Fig. 11). Both stalk and head are nearly cylindrical but are more convex abaxially; the head sits obliquely on the stalk. Vascular tissue is absent. Necrotic cells on gland tips of older leaves may show that glands gradually cease to function once the leaves mature (see also Lapinuro 1976).

In the closely-related Apocynaceae, the gland secretion is thought to be a high polymer resin and its suggested role is to provide a protective coating on adjacent young lateral buds

(Ramayya & Bahadur 1968); this may apply also in *Marsdenia* and *Rhyncharrhena*. Such coatings might protect against climatic extremes in arid areas (Dell & McComb 1978) or against herbivores (Juniper & Jeffree 1983).

The anatomy and morphology of the glands are very similar to those of the other taxa examined in detail, both Apocynaceae (Ramayya & Bahadur 1968) and the asclepiad *Marsdenia liisae* (Lapinuro 1976, Williams 1989).

GERMINATION

Methods

The coma was removed from seeds of known age and provenance (Appendix 2) and any broken, shrivelled or empty seeds discarded. Seeds were surface sterilized in 3% sodium hypochlorite and sown onto 9 cm Whatman 182 filter papers in sterile glass petri dishes, with five replicates of ten seeds per dish. The dishes were placed in growth cabinets with lights supplying 180–240 μ E m⁻² s⁻¹ for a 12 hr photoperiod at 10/10°C, 16/14°C, 25/15°C and (*Marsdenia* only) 30/20°C. For *Marsdenia* only, seed of four ages (Appendix 2) stored at room temperature and humidity was tested for germinability at 25/15°C. Comparable *Rhyncharrhena* seeds were not available.

Results and discussion

No seeds germinated at 10/10°C. For *Marsdenia*, final germination percentage was very similar at 25/15°C and 30/20°C but the germination rate was faster at 25/15°C. By comparison, 16/14°C reduced both the amount and the rate of germination in both species. Germination was highest and fastest in *Rhyncharrhena* at 25/15°C (Fig. 13).

Germinability of *Marsdenia* seed declined steeply with time and was zero at 14 yr (Fig. 14).

The germination maximum of 25/15°C for *Marsdenia* is broadly similar to that for other asclepiads like *Morrenia odorata* (20–25°C; Singh & Achhireddy 1984) and *Ampelamus albidus* (30°C; Soteres & Murray 1981). The present data for 10/10°C and 16/14°C suggest that germination may be reduced or prevented by winter temperatures in the field. All viable seeds of both species tend to germinate quickly given appropriate conditions; there is no evidence of dormancy as in some cool temperate species like *Asclepias syriaca* (Bhowmik & Bandeen 1976).

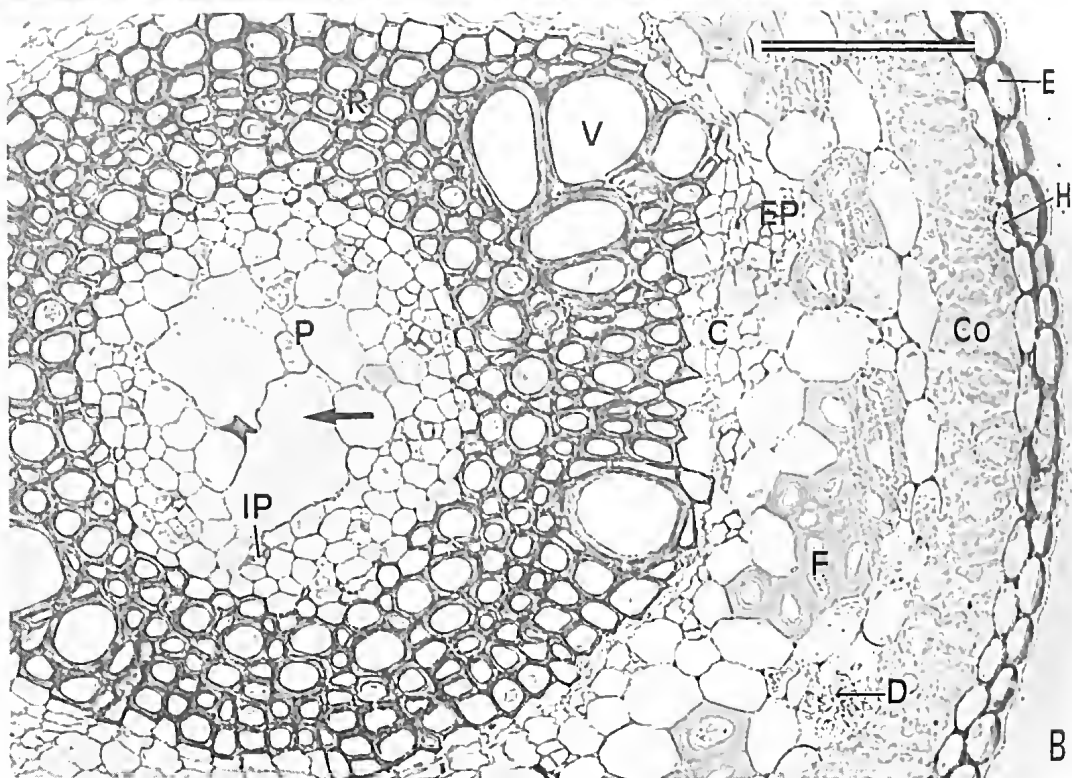
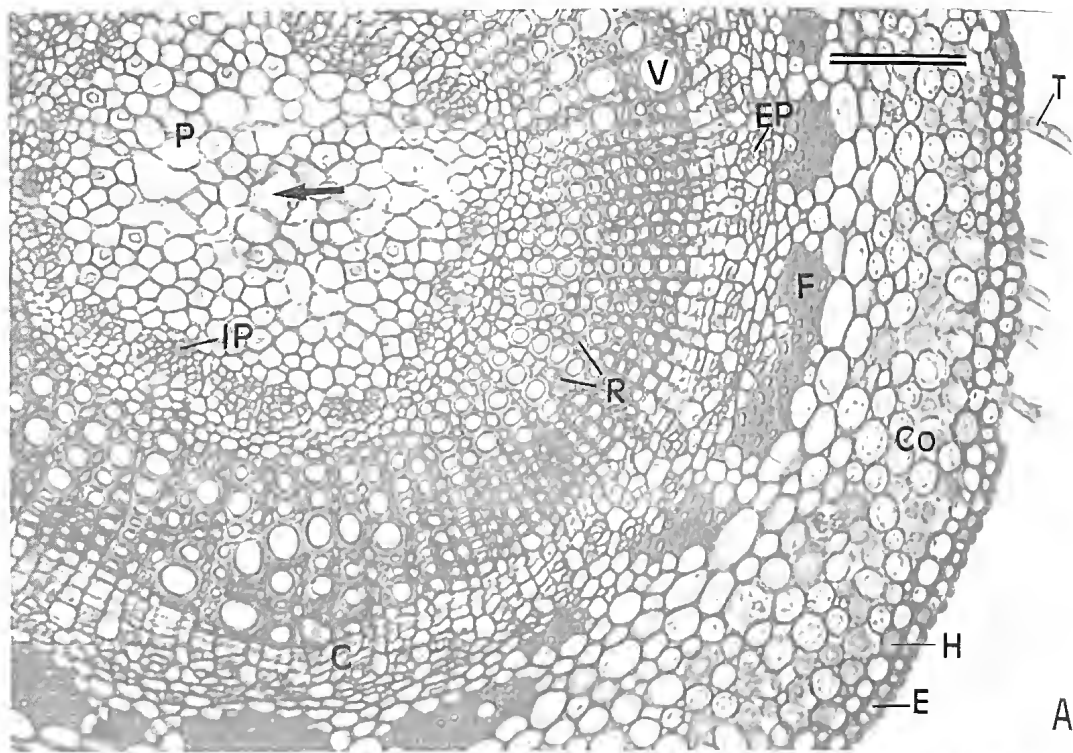


Fig. 10. Transverse sections of lower stems from approximately 18 week-old plants of *Marsdenia australis* (A) and *Rhyncharrhena linearis* (B), showing thick-walled epidermis (E) and hypodermis (H), trichome (T; cut short in sectioning), cortical chlorenchyma (Co), a druse (D), external phloem (EP) and phloem fibres (F), secondary xylem with vessels (V) and thickened rays (R), internal phloem (IP) and pith (P) with lysigenous cavities (arrowed). Scale bars = 0.1 mm.

The fast germination found here is similar to that found for a range of dry-country succulent asclepiads (Harp 1987).

SEEDLING GROWTH

Methods

Seedlings 5 to 15 days old were planted one per pot into 80 × 150 mm pots containing two parts sandy loam, one part vermiculite and one part perlite with controlled release fertilizer ('Nutricote', Chisso Asahi Co. Ltd, Tokyo, Japan) at the recommended rate. There were 10 replicates × 2 species × 2 treatments (16/14°C and 25/15°C). Otherwise growth cabinet conditions were as for the germination trials except for a 14 hr photoperiod. The seedlings were moved into the cabinets after four weeks at 25/15°C. None was given a support to climb on. All plants were dry-weighted at 105°C at an age of 18 wk.

Results and discussion

For all plants of both species introduced to 16/14°C, shoot growth rapidly slowed and then stopped. By contrast, 25/15°C produced rapid growth, with shoot length more than twice as long in *Rhyncharrhena* but shoot dry weight very similar in both species (Table 2). At 18 weeks, the *Marsdenia* seedlings at 25/15°C already had a well-developed tuberous root system while *Rhyncharrhena* had much thinner, non-tuberous roots. This difference correlated with much higher *Marsdenia* root dry weight which in turn resulted in higher total dry weight for that species (Table 2). While *Marsdenia* root weight increased 6.5 times from 16/14°C to 25/15°C, *Rhyncharrhena* increased less than twice. At 16/14°C the tubers of *Marsdenia* were very poorly developed. How this relates to climate and drought survival in the field requires further work.

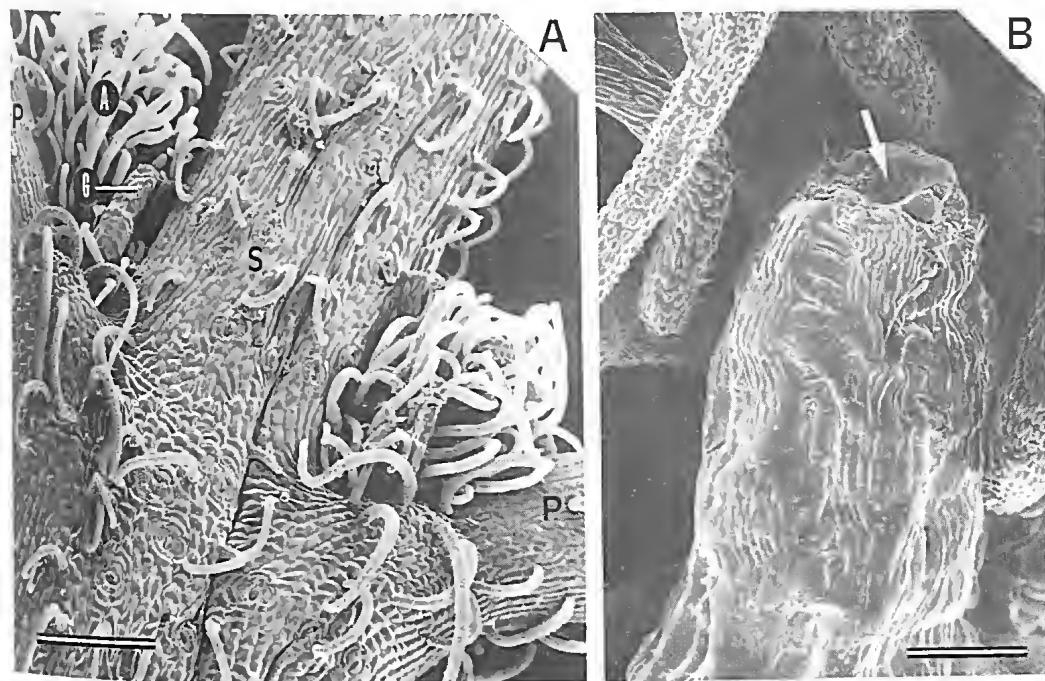


Fig. 11 A, scanning electron micrograph of a *Rhyncharrhena linearis* node, showing stem (S), petiole (P), axillary bud (A) and foliar gland (G). Scale = 0.03 mm. B, head of gland showing pore (arrowed). Scale = 0.3 mm.

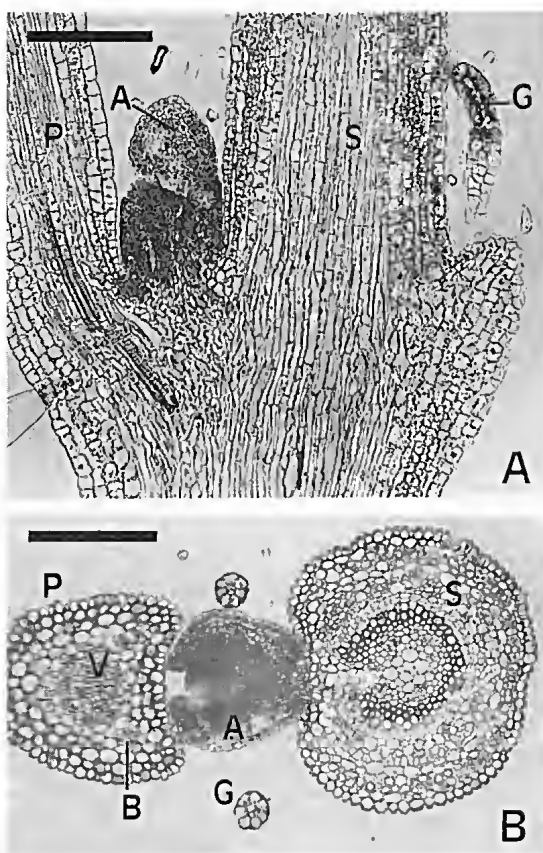


Fig. 12. A, longitudinal section through a stem node of *Rhyncharrhena linearis*, showing stem (S), petiole (P), an axillary bud (A) and a foliar gland (G) on the base of the opposite petiole. Scale = 0.2 mm. B, transverse section through a similar node, showing stem (S), axillary bud (A) and foliar gland stalk (G). The petiole (P), cut obliquely, has a crescent-shaped vascular strand (V) and accessory bundles (B). Note the radial arrangement of cells in the gland. Scale = 0.2 mm.

In summary, there are striking differences in seedling growth between the two species. The extra dry matter produced by *Marsdenia* is used for production of tuberous roots. Despite very similar shoot dry weights, *Marsdenia* produces thicker stems, larger leaves and a more rigid, erect shoot while *Rhyncharrhena* produces much longer, thinner shoots (Fig. 15). The reasons for these differences are obscure given the similarity between the two species in behaviour and habitat in the field.

The cessation of growth of both species at 16/14°C is like the behaviour of C_4 grasses at such temperatures (Evans et al. 1964). Given

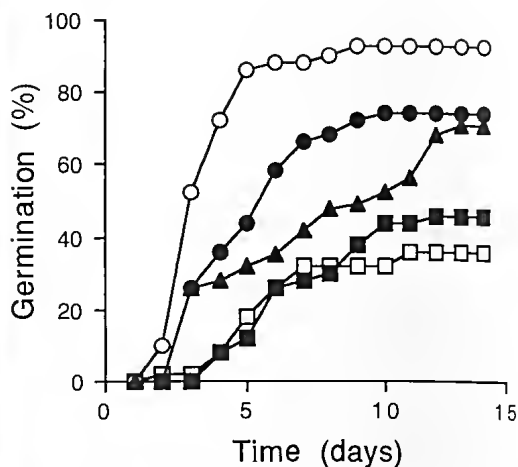


Fig. 13. Germination rate of *Marsdenia australis* and *Rhyncharrhena linearis* at various temperature regimes for seed 19 mo old. Open circles = *Rhyncharrhena* at 25/15°C, open squares = *Rhyncharrhena* at 16/14°C. Closed triangles, circles and squares = *Marsdenia* at 30/20°C, 25/15°C and 16/14°C respectively.

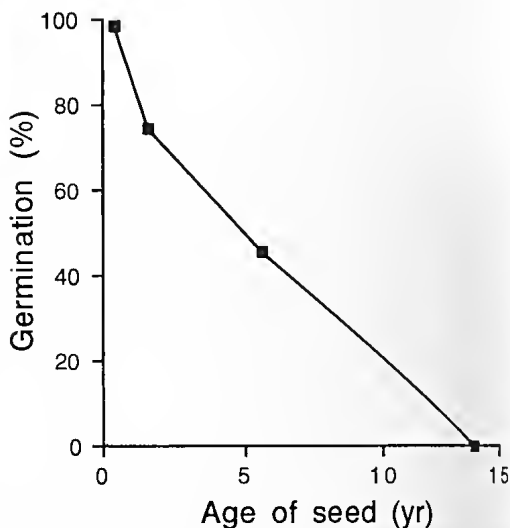


Fig. 14. Germinability of *Marsdenia australis* seeds of various ages at 25/15°C.

that the mean daily maximum temperature in June is about 16°C, the data suggest that little or no growth will occur in winter in the field. This is discussed further below.

These unsupported seedlings bowed over and grew more-or-less horizontally once they reached heights of 150 mm or so. We lack data

	<i>Marsdenia</i>		<i>Rhyncharrhena</i>	
	16/14°C	25/15°C	16/14°C	25/15°C
Shoot length (mm)	66	436	199	1142
Dry weight (g)				
Shoot	0.14	1.57	0.15	1.58
Root	0.29	1.89	0.38	0.71
Total	0.43	3.46	0.53	2.29

Table 2. Mean shoot length and dry weight of 18 wk old *Marsdenia australis* and *Rhyncharrhena linearis* seedlings at two temperature regimes.

for supported young plants except for a single *Marsdenia* plant which twined 1.1 m up a stake in 10 weeks. Possible effects on growth caused by provision of support need investigating.

PHENOLOGY

Methods

General observations were made at all sites. At site 1, from 13 February to 23 May 1990, effects of water supply on shoot growth and flowering were studied by watering two *Marsdenia* and three *Rhyncharrhena* plants with a total of 600 L per plant via 22 L containers feeding a dripper system running at 400 mL/hr. Watering stopped

in May when rainfall had clearly provided available water in the topsoil. Six unwatered control plants were monitored per species.

At site 2, from 19 February to 6 April 1990, one *Marsdenia* and three *Rhyncharrhena* were given 150 L of water each. One *Marsdenia* and three *Rhyncharrhena* were monitored as unwatered controls.

All plants monitored at sites 1 and 2 were more than 0.8 m high and were supported by shrub canopies. From 2 to 6 shoots per plant were tagged initially. Shoots were monitored until September 1990. Unfortunately it was logistically impossible to provide continuous watering to a larger number of plants. This factor, plus death of and damage to some shoots, produced very low replication in some cases, reducing the value of the experiment. Only a summary of the results is given below.

Results

Flowering and fruiting. Observations in the Red Cliffs district on similar numbers of plants of each species from 1981 to 1990 gave a flowering time range of October to March for *Marsdenia* and February to May for *Rhyncharrhena*. For the latter, however, buds can sometimes be seen even in July and September and we think it likely that flowering can occur from October to May (see also Cunningham et al. 1981, Jones & Gray 1988). In general, flowering for both occurs in the warmer months, especially when significant rain has fallen previously. However, *Marsdenia* is more likely to exhibit plentiful general flowering in December–January under a wide range of rainfall regimes. *Rhyncharrhena* seems to have a less definite flowering period; it seems more opportunistic, reacting more quickly with vigorous growth and flowering after significant summer–autumn rains. This species difference is dealt with more fully below. The smallest plants of both species seen flowering were about 600 mm high.



Fig. 15. Seven-week-old seedlings of *Marsdenia australis* (left) and *Rhyncharrhena linearis* (right) grown in a growth cabinet at 25/15°C.

It is much more common for flowers of both species to wither and fall than to produce fruit; this can happen to *Rhyncharrhena* when *Marsdenia* is still flowering and fruiting at the same site. Although *Rhyncharrhena* flowered a number of times from 1981 to 1990, only five fruits (containing a total of 177 seeds) could be found, one in 1982 and four in 1989–90. Other than this, the only *Rhyncharrhena* fruiting records we know of are: (a) June 1950, after exceptional February–March rainfall of 177 mm (E. Ramsay, unpublished manuscript); and (b) March 1976, after exceptional October–December rainfall of 225 mm (our data). Finding as many as four fruits in 1989–90 was not due to heavy rain but because we started to examine repeatedly 48 adult plants; (a) and (b) above may indicate that appreciable levels of fruiting only follow exceptional rains.

Marsdenia fruiting is more common; for example 18 fruits could be found in 1984 and in 1990 38 adult plants under observation produced 15 fruits.

Number of seeds per fruit ranged from 37 to 213 for *Marsdenia* and 18 to 78 for *Rhyncharrhena*. Individual *Marsdenia* flowers remain open for seven to ten days and those of *Rhyncharrhena* for two to three days. This compares with five to six days for *Asclepias meadii* (Betz 1989), seven to eight days for *A. tuberosa* (Wyatt 1981) and 10–15 days for *Fischeria funebris* (Skutch 1988).

General phenology, 1989–1990. Following rain falls of 125 mm from 14 March to 7 April 1989, *Rhyncharrhena*, but not *Marsdenia*, flowered in mid-April. Virtually all these flowers were shed in late April without setting fruit.

No further flowering of either species occurred until above-average rain of 54 mm from 6 November to 2 December. By 14 December, shoot growth and flowering occurred profusely in all full-grown *Marsdenia* plants but not in any *Rhyncharrhena* plants.

In this area, 10 mm is the minimum rainfall that most farmers regard as being significant for plant growth in summer. There were no falls this large between 3 December 1989 and 21 April 1990. On 2 January 1990, with temperature maxima about 40°C, all *Rhyncharrhena* plants were either wilted or had started losing leaves. This was not true of *Marsdenia* except for some wilted sucker shoots. However, on 3 January 1990 temperatures reached 47°C, the hottest for 50 years; nearly all *Marsdenia* wilted and shed

their flowers except for those at site 3. The plants at site 3 shed most of their flowers a few days later. By 11 January, most *Marsdenia* shoots had recovered without damage. Between then and 25 January new shoot growth was noted for *Marsdenia* but not for *Rhyncharrhena* which showed further leaf loss and stem death and did not recover until April.

It was possible to obtain a few mature fruits of both species in January 1990; those of *Rhyncharrhena* probably arose from the April 1989 flowering while the origin of the *Marsdenia* fruits is unknown.

Detailed studies. At site 1, small flower buds were present on some plants of both species, especially *Rhyncharrhena*, before watering started. A second crop of *Rhyncharrhena* buds was present on 15 May following substantial rains. Despite these buds, throughout the work only a single plant of either species was seen with open flowers, a *Rhyncharrhena* in early March, and no fruit was set. Plants of both species, both watered and unwatered, showed some increase in shoot length and leaf number from February to September. This was most marked during April and May. The overall increases in mean shoot length to 4 August 1990 were: *Rhyncharrhena* (watered) 473 mm, *Rhyncharrhena* (unwatered) 133 mm, *Marsdenia* (watered) 197 mm and *Marsdenia* (unwatered) 229 mm. Although there was no statistically significant effect of watering, more data may have confirmed that *Rhyncharrhena* responds more strongly to watering than *Marsdenia*.

Events at the other sites from February to September 1990 were generally similar to those at site 1. The very few *Rhyncharrhena* that flowered included two plants at site 2 on 22 March, possibly in response to the artificial watering. The only *Marsdenia* to flower were three plants at site 5 on 6 March following 17 mm of rain. Despite the widespread *Marsdenia* flowering of December 1989, only at site 3 did fruit set occur, with a total of 10 fruits. A fruit cut open in June contained only immature seeds, while seeds from one cut open in August gave 100% germination. The remaining fruits finally opened naturally in mid-November 1990. This period of 11 months from flowering to seed release compares with two to four months from flowering to fruiting for *Sarcostemma esculentum* and *Gymnema geminatum* (Forster 1989) and about 3.5 months from pollination until fruits are ripe in *Asclepias meadii* (Betz 1989).

The period from pollination to seed release for three species of *Asclepias* ranges from about 2 to 4.5 months (Kephart 1987).

With increasing temperatures in September, most mature *Marsdenia* and *Rhyncharrhena* plants produced new crops of flower buds. The driest spring on record ensued (15 mm of rain at Mildura) and December was also very dry (4 mm). All *Rhyncharrhena* flower buds were lost but *Marsdenia* showed widespread flowering by mid-November. With very high January rainfall (87 mm), some flowers produced a crop of fruits 5 mm in diameter by 12 January and these became virtually full-sized by 2 February. A total of 49 full-sized fruits were counted at sites 1 and 3 on 13 February 1991.

By contrast, it was only after the 29 mm of rainfall on 5 January that *Rhyncharrhena* flowered (Fig. 16). It is assumed that this flowering produced the 20 well-developed fruits found at site 1 on 11 February. In central Australia, for both species, "significant fruiting only occurs after exceptional seasons or after fire" (P. K. Latz, personal communication).

The timing of events in *Marsdenia* is consistent over large areas; around Lindsay Point, 115 km to the west-north-west, *Marsdenia* also shed its seeds and flowered in November 1990 (R. Stoeckel, personal communication).

A major difference between *Marsdenia* and *Rhyncharrhena* is that in hot, dry periods during summer and autumn 1990 virtually all *Rhyncharrhena* plants lost at least some of their leaves, while no *Marsdenia* plants did. This was even more noticeable in the very dry late spring of 1990 when the few remaining *Rhyncharrhena* leaves were yellow and wilted while all *Marsdenia* leaves were still present and in good condition. The partial deciduousness of *Rhyncharrhena* may aid survival during drought (Russell-Smith & Dunlop 1987). While *Marsdenia* is regarded by Pate & Dixon (1982) as semi-deciduous if drought-stressed, we have never seen leaf loss at any time. Perhaps leaf loss occurs only in the most extreme conditions, possibly as a prelude to stem death (P. K. Latz, personal communication).

Although it is said that *Rhyncharrhena* can be

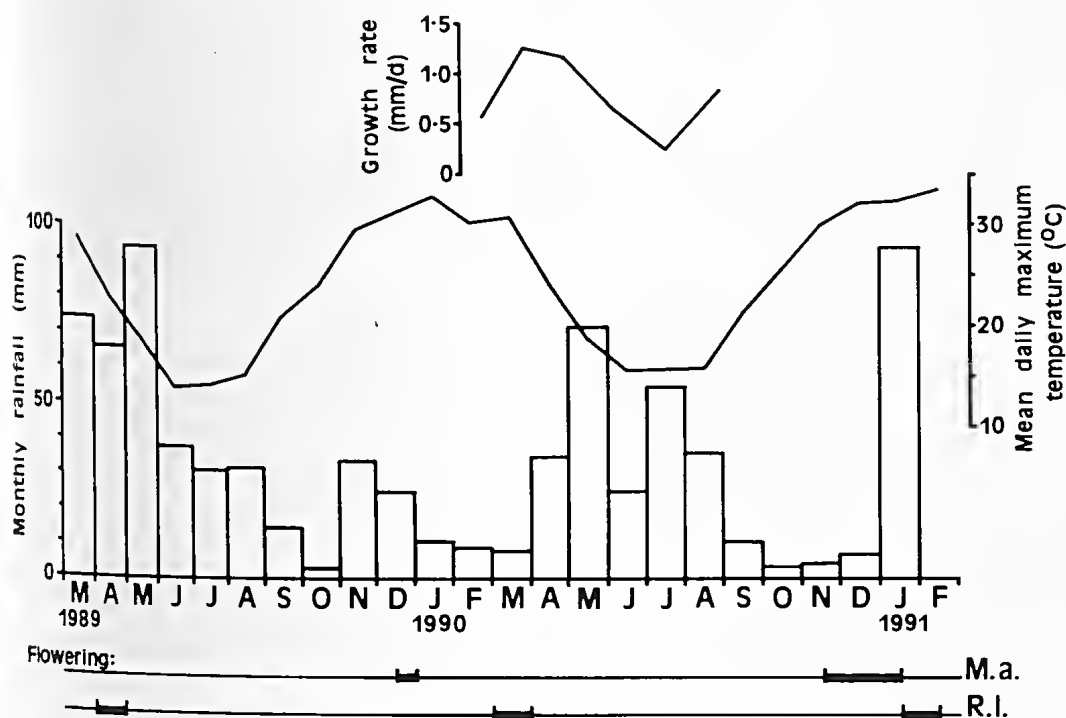


Fig. 16. Monthly rainfall (Red Cliffs), monthly means for daily maximum temperatures (Mildura), flowering times for *Marsdenia australis* and *Rhyncharrhena linearis*, and growth rate (shoot elongation) for unwatered *R. linearis* shoots at site 1 from February to September 1990.

short-lived in cultivation (Jones & Gray 1988), one of us (JHB) has observed individual plants of both species at Red Cliffs for more than 20 years. There has been no apparent size increase. It is possible that such plants may be very long-lived like those of other clonal species (Janzen 1975).

Discussion

Our observations suggest that some shoot growth occurred throughout the February–August period but that this was slow at the start and the finish, presumably due to low soil moisture and low temperatures respectively. Presumably shoot growth stops completely in very dry conditions like November–December 1990. Shoot growth is clearly much more vigorous in summer after thunderstorms or general rain than at other times.

In colder areas of southern Australia, introduced species of *Asclepias* are said to “die back when (night) temperatures drop below 0°C” and so to “disappear over winter” (Zalucki 1986). In our 1990 work, *Marsdenia* and *Rhyncharrhena* did not show any frost damage in a winter when the lowest absolute minimum screen temperature at Mildura was –1°C. Both are said to be tolerant of light to moderate frosts (Jones & Gray 1988). However, for *Marsdenia*, “foliage may dry off after frosts” (Griffin 1985), and in the winter of 1985 plants of both species growing on a fence at Sunny Cliffs showed frost damage while *Marsdenia* plants growing inside shrubs nearby were unaffected (personal observations).

The two species were strikingly different in flowering behaviour. In *Marsdenia* flowering (and fruiting) occurs on a much higher proportion of plants than in *Rhyncharrhena*. There was regular November–December flowering of *Marsdenia*, even in very dry conditions, whereas *Rhyncharrhena* flowering only followed heavy rain. It is not known why heavy autumn rain can produce flowering of *Rhyncharrhena* but not *Marsdenia*, as in 1989. In Queensland rainforest “almost all liane species flower once a year, in early summer” (Hegarty 1988). If individual *Marsdenia* plants flower annually, summer flowering would mean that few or no plants would flower in the succeeding autumn. Neither species flowers or fruits in the cold conditions of winter; it seems that amount of fruiting is related to rainfall at other times, especially summer. For both species, rainfall can be sufficient to produce flowering but be insufficient for any subsequent fruiting to occur.

Marsdenia flowering phenology was categorized by Pate & Dixon (1982) as “flowers produced annually during growth season”.

It was hoped that artificial watering would produce widespread flowering and even fruiting, at least of *Rhyncharrhena*, but it only contributed to very limited flowering of that species. Watering a few shoots might not produce marked changes if those shoots were part of a very large clone covering most or all of the site, as is quite possible.

For both species, large numbers of sucker shoots up to 300 mm high can appear in open areas adjacent to mature plants. This is especially true in wet years like 1974–5, but plenty were found also in 1990 (Table 1). Before site 4 was fenced, *Rhyncharrhena* sucker shoots were grazed right off for three successive years; probably by kangaroos (T. Dominelli, personal communication). However, in unstocked areas near Red Cliffs lacking kangaroos and rabbits, large numbers of *Rhyncharrhena* suckers can appear after rain and then totally disappear during dry conditions, as they did in December 1990. In *Marsdenia*, only the smallest suckers die off during drought.

Most such suckers are found in open areas, often on perennial grasses or on live or dead annuals, but also in completely bare areas. In *Marsdenia*, such suckers can remain small but be many years old. For both species, in the absence of a substantial aerial support the suckers remain as small single shoots or die back; they do not form large, mature plants of shrub or creeper growth form, unlike *Jasminum didymum* (Cunningham et al. 1981, Hegarty & Clifford 1984).

Casual observations of supported and unsupported seedlings (see seedling growth section above) suggest the potential for very rapid height growth responses to provision of support, as is the case for rainforest lianes (Putz 1984).

Some of the striking phenological differences between *Marsdenia* and *Rhyncharrhena* may be because storage material in the tuberous roots of *Marsdenia* allows it to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Work is needed to compare the water potential and intrinsic cellular resistance to desiccation of both species.

FLORAL BIOLOGY

Despite repeated observations, pollinators could not be found visiting flowers of either species. *Rhyncharrhena* is one of a number of asclepiads which has dark purple flowers (Good

1956). This feature and the presence of vibratile hairs on the flowers suggests that pollination may be by flies (Whittington 1989). Both *Marsdenia* and *Rhyncharrhena* flowers are odourless, at least in daytime.

All species in the family Asclepiadaceae studied in detail are obligate or nearly obligate outbreeders and exhibit low rates of fruit set, typically one to five per cent (see e.g. Holm 1950, Woodson 1954, Skutch 1988). These low rates can be related to low pollination rates and to energy limitation causing abscission of pollinated flowers and pod abortion (see e.g. Cabin et al. 1991, Pleasants 1991). Low rates of fruit set certainly apply also to *Marsdenia* and *Rhyncharrhena*. For a threatened prairie species of *Asclepias* now restricted to a few tiny refugia surrounded by farmland, problems may arise from (a) low populations of insect pollinators, and (b) insufficient plants to attract pollinators and maximize cross-pollination. Problem (b) can be exacerbated by extensive clones of the species causing extensive self-pollination (Betz 1989). These same problems may apply to many isolated *Marsdenia* and *Rhyncharrhena* stands in largely cleared Victorian areas.

Work on *Asclepias quadrifolia* shows that plants under the threshold of 330–340 mm stem height are unable to mature a fruit, any fruits initiated being aborted. Many small flowering plants apparently lack the energy resources to mature a fruit; only 20% of the flowering plants produce a fruit, production of which clearly depletes the plant's energy reserves (Chaplin & Walker 1982). *Marsdenia* and *Rhyncharrhena* seem to exhibit similar behaviour.

RESPROUTING

Fifty days after germination, ten plants each of *Marsdenia* and *Rhyncharrhena* were cut off below the cotyledons. Eight *Marsdenia* plants and all the *Rhyncharrhena* plants had resprouted 14 days later. Similarly, resprouting can occur in cut off 21-day-old *Asclepias syriaca* seedlings (Bhowmik & Bandeen 1976).

Patches of *Marsdenia* are known to persist in some areas of Victoria cleared of native vegetation in the 1920s; the small sucker shoots are repeatedly destroyed by ploughing or stock grazing but new ones continue to be produced by resprouting (J. N. Macfarlane, personal communication). Similar behaviour occurs in asclepiad weeds like *Asclepias syriaca* (Bhowmik & Bandeen 1976) and *Morrenia odorata* (Tucker & Phillips 1974). Such resprouting behaviour also

means that *Marsdenia* and *Rhyncharrhena* can occasionally be found climbing among the trees in commercial citrus groves, where irrigation can cause them to fruit prolifically (J. N. Macfarlane personal communication). Analogously, the asclepiad *Morrenia odorata* is a major weed of Florida citrus groves (Tucker & Phillips 1974).

Post-fire behaviour of *Marsdenia* and *Rhyncharrhena* has not been seen in Victoria. In central Australia, vigorous resprouting can make both species conspicuous after fire, they being among the first species to appear. Later in the post-fire period, increased competition from other perennial species can make them less conspicuous and reduce or prevent their fruiting (Latz 1982 and personal communication). Resprouting allows other asclepiads to tolerate frequent low-intensity fires in monsoon areas further north (Russell-Smith & Dunlop 1987).

RESPONSES TO GRAZING

The Asclepiadaceae is noted for presence of toxic cardiac glycosides, alkaloids and resinoids. As a result, many species are extremely unpalatable to grazing mammals and are generally avoided by them (Everist 1974). For example, severe overgrazing by goats can produce monospecific communities of the poisonous asclepiad *Calotropis procera* (Kassas 1966). Despite this, it is thought that mammal grazing can dramatically reduce *Marsdenia* and *Rhyncharrhena* populations. In Victoria, by 1937 *Marsdenia* was "rapidly becoming rarer" because it was especially palatable to rabbits, which ate the foliage and removed the bark from stems near the ground (Zimmer 1946).

Both species are now very rare virtually throughout their former range in Victoria (see Table 1). For example, only two adult plants of *Marsdenia* are now known in Hattah-Kulkyne National Park and there are only three recent records from the whole of the Sunset Country. The only populations of any size are from unstocked areas close to towns (sites 1 and 3, Red Cliffs; site 5, Walpeup) where rabbit (and other grazing mammal) numbers remain low, possibly due to factors like predation from domestic cats and dogs. *Rhyncharrhena* behaves similarly (Table 1). In some parts of the ranges of both species, grazing by hares may be more important than that by rabbits (J. N. Macfarlane personal communication).

In western New South Wales *Rhyncharrhena* is grazed readily by sheep. Under grazing "the

only plants which appear to survive are those which have the stem closely pressed to the bark of a tree or are growing up through a groove in the bark" (W. E. Mulham, personal communication). In central Australia *Marsdenia* is noticeably rarer in the area of highest rabbit numbers, namely the south west corner where rabbit grazing has apparently severely reduced the species (Latz 1982).

A similar case of a marked grazing effect on a liane concerns the eastern Victorian *Parsonsia brownii* in the closely related family Apocynaceae. *P. brownii* is especially palatable to wallabies and normally only scattered plants of it can be found. Where wallabies are absent, however, as in some very small remnants of native vegetation or in reserves surrounded by suburbs, dense stands of *P. brownii* develop (Ashton 1989; N. H. Scarlett, personal communication). The New Zealand *P. heterophylla* is especially palatable to a browsing bird (Clout & Hay 1989).

DISPERSAL

Both *Marsdenia* and *Rhyncharrhena* have typical asclepiad seeds with a terminal coma of long hairs. In *Asclepias syriaca*, these hairs allow wind dispersal at distances of up to 150 m and further (Morse & Schmitt 1985), and in *Araujia sericifera* such dispersal allows the species "to arrive in almost every Auckland garden" (Esler 1988). There is no evidence that *Marsdenia* or *Rhyncharrhena* seeds are predated by birds or ants.

CONSERVATION

While not threatened Australia-wide, both *Marsdenia* and *Rhyncharrhena* are now regarded as vulnerable in Victoria (Gullan et al. 1990). The apparent severe decline under grazing, the absence of seedling establishment, the lack of information on the lifespan of the remaining adult plants and the very small number of adults in biological reserves are all causes for concern. Although *Rhyncharrhena* is recorded from a total of four Victorian reserves (Beaughole 1979), in each case only a few plants are present (A. C. Beaughole and J. N. Macfarlane, personal communications). *Marsdenia* is a very similar case, being regarded even in 1937 as "likely to become extinct" (Zimmer 1946).

Conservation work so far has involved fencing small patches of both species at Hattah-Kulkyne

National Park (site 4) and Pink Lakes State Park (site 6), and at the latter providing small tree guards about 300 mm high for *Rhyncharrhena* suckers. We only saw fruiting of either species occur when the plants were climbing in shrubs or trees; although increased shoot growth occurred when the tree guards were installed, no fruit was set. Grazing exclosures for the species should include long-lived trees or shrubs if possible; if none are present, it may be necessary to introduce them to make the exclosure worthwhile in the long-term.

ETHNOBOTANY

In central Australia *Marsdenia* and *Rhyncharrhena* were important and favoured aboriginal foods, all parts being used except the stems and fine roots. The aborigines were aware that a diet containing a high proportion of *Rhyncharrhena* caused their children to lose weight (Latz 1982). The ground-up seeds of both species are reputed to have been used as an oral contraceptive (Lassak & McCarthy 1983).

The immature fruits of *Marsdenia* are so delicious that the species may be worthwhile cultivating (Cherikoff & Isaacs, no date; V. Cherikoff, personal communication).

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APPENDIX 1

Location of the study sites; see also Table 1.

Site 1. 34°20'S, 142°20'E. All plants studied were less than 50 m W of Campbell Avenue. *Rhyncharrhena* sites on ridge 0.3 km N of 22nd Street. *Marsdenia* sites on ridge 0.3 km farther N.

Site 2. 34°21'S, 142°21'E. W side of main N-S track through reserve, 0.1–0.3 km SE of the intersection of the track and Woomera Avenue.

Site 3. 34°48'S, 142°17'E. S side of Nardoo Street, Red Cliffs. The plants are scattered through the least disturbed area.

Site 4. 34°48'S, 142°17'E. (a) *Marsdenia*. Plot 0.6 km along Jasmine Track from its N end, then 0.2 km WSW of track. (b) *Rhyncharrhena*. National Parks Service plot no. 9E, 0.8 km along Jasmine Track from its N end, then 28 m W of track.

Site 5. 35°10'S, 142°2'E. In the western block of the reserve, 0.5 km S of Ouyen Highway down W boundary track just E of where it meets E–W track.

Site 6. 35°1'S, 141°45'E. (a) *Marsdenia*. Plot near SE corner of Lake Crosby, 0.2 km along Campground Track from its S end, on NE side of track. (b) *Rhyncharrhena*. Plot near S tip of Lake Kenyon, 0.5 km along Lake Kenyon Track from its W end.

APPENDIX 2

Seed sources used

- a) The germination/seed age trial (all *Marsdenia*).
 1. 22 June 1976. Huckitta Station, Northern Territory.
 2. 30 October 1984. Railway and road reserve on W side of Calder Highway where it meets 22nd Street, about 4 km N of Red Cliffs.
 3. 22 October 1988. As for 2 above.
 4. 27 January 1990. Site 1 (Appendix 1).
- b) The germination/temperature trial used no. 3 above and the seedling growth trial used no. 4. All *Rhyncharrhena* seeds used were collected at site 1 (Appendix 1) on 25 January 1990.

SPAWNING OF THE MOUNTAIN GALAXIAS, *GALAXIAS OLIDUS* GÜNTHER, IN BRUCES CREEK, VICTORIA

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O'CONNOR, W. G. & KOEHN, J. D., 1991:12:31. Spawning of the mountain galaxias, *Galaxias olidus* Günther, in Bruces Creek, Victoria. *Proceedings of the Royal Society of Victoria* 103 (2): 113-123. ISSN 0035-9211.

In Bruces Creek, Victoria, *Galaxias olidus* had a spawning season extending from early August to late October. Water temperatures ranged between 8° and 10.2°C over this period. Fertilized eggs were mainly found attached to the underside of boulders in riffles but some eggs were also found lodged amongst substrate or drifting downstream. *G. olidus* had a relatively low fecundity with an average of 198 eggs per female. Average egg diameter was 2.3 mm. All *G. olidus* were mature in their second year, although males matured earlier than females. The population had an overall sex ratio of 1:1 but the sexes were unevenly distributed, with more males in 0+ and more females in 2+ and 3+ year classes. The preferred habitat of adults was in pools. Fertilized eggs collected from the stream at an early stage of embryonic development hatched in the laboratory after 21 days at temperatures between 12.9° and 14.8°C. Newly hatched larvae averaged 9.4 mm in length.

THE MOUNTAIN GALAXIAS, *Galaxias olidus* Günther, a small (less than 145 mm long) native freshwater fish of the family Galaxiidae (McDowall 1980a), is generally found in small, headwater streams (Berra 1973, Fletcher 1979, Jackson 1981) at altitudes up to 1800 m (McDowall & Frankenberg 1981). The species occurs from southern Queensland to south-eastern South Australia (Merrick & Schmida 1984), although it has been recognized as having a highly fragmented distribution, often occurring in small isolated populations (Tilzey 1976, Cadwallader 1979, Jackson & Davies 1983, Cowden 1988).

G. olidus is widespread throughout Victoria (Cadwallader & Backhouse 1983), where its conservation status is "indeterminate" (KoeHN & Morison 1990) due to uncertainty about the taxonomic status of the various taxa in this species complex. The population of this complex occurring in Bruces Creek conforms to the "typical" *G. olidus* form (see Cadwallader & Backhouse 1983). Although most of this taxon is common and widespread, *G. olidus* var. *fuscus* has been categorized as endangered in Victoria (KoeHN & Morison 1990) and nationally (Jackson 1991).

Until recently there had been little investigation of the life history of *G. olidus* (KoeHN & O'Connor 1990a). Most information remains unpublished in university theses (Harasymiw 1970, Fletcher 1979, Cowden 1988, Drayson 1989). The present paper contains information

on the spawning of *G. olidus* in a small Victorian stream and includes data on habitat, population structure, sexual maturity, fecundity, spawning season and site, egg description, incubation period, and description of larvae.

STUDY SITE

The study was conducted in the upper reaches of Bruces Creek, Victoria, approximately 47 km north-east of Melbourne (Fig. 1), where McKenzie & O'Connor (1989) found a large population of *G. olidus*, the only fish species present. The absence of other species, particularly predatory species such as brown trout, *Salmo trutta*, was considered important as it allowed instream distribution and habitat preferences to be unaffected. *S. trutta* has been implicated in the displacement of *Galaxias olidus*, *G. truttaceus* and *G. brevipinnis* from preferred habitat areas (KoeHN unpubl. data).

Bruces Creek rises on the western slopes of Mt Disappointment in the Great Dividing Range and flows firstly in a southwesterly then southeasterly direction to its confluence with the Plenty River. The study site was about 6.5 km downstream from the source of Bruces Creek at an altitude of 340 m. At the site, Bruces Creek is a small, shallow, third order stream with an average width of 2.0 m, an average depth of approximately 0.3, and consisting of alternating pools and riffles. The stream is in a relatively natural

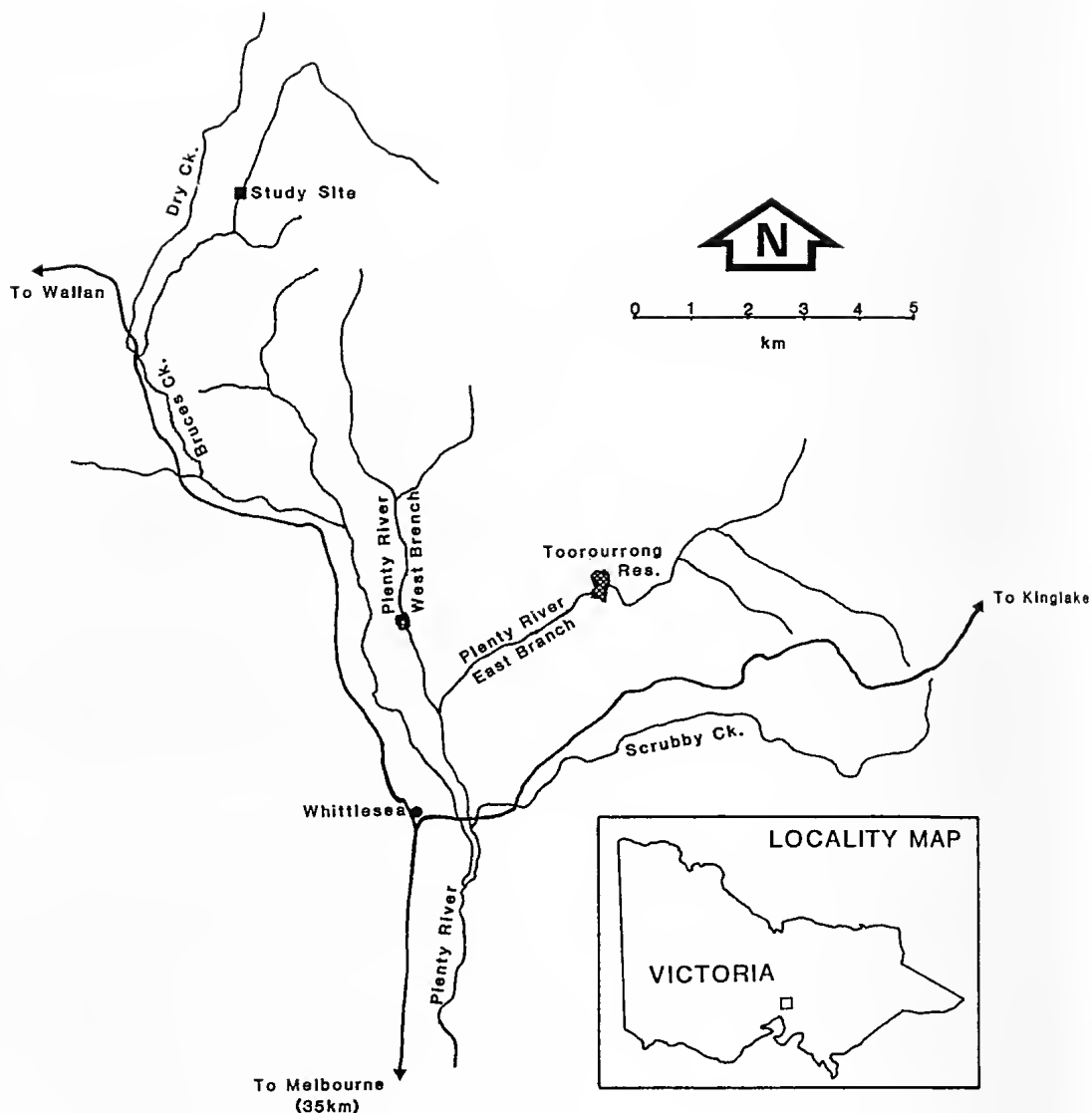


Fig. 1. Map showing the study site at Bruce's Creek.

condition and contains abundant instream cover and wood debris.

Beardsell (pers. comm.) described the bank vegetation at the site as mountain grey gum riparian damp sclerophyll forest (with no alien flora species) and the hillside vegetation as dry sclerophyll. The surrounding land is State Forest.

METHODS

G. olidus was collected from Bruce's Creek on 11 occasions between 15 August 1990 and 25 Octo-

ber 1990 to examine spawning condition. This sampling period was selected as it coincided with previously reported spawning periods (Koehn & O'Connor 1990a). The length of stream fished for each sample ranged from 15 m to 60 m, and the number of fish collected in each sample varied from 22 to 62. Samples were taken over a 380 m stretch of stream, with only one section being sampled on each occasion. On 11 July 1991 an additional 24 ripe female fish were collected to determine egg numbers.

An estimate of the proportion of fish collected from pools and riffles was made during these

collections. On 4 October 1990 and 25 October 1990 sampling was conducted to determine population densities and on 11 July 1991 an additional 43 m stream section containing 5 pools and 4 riffles was sampled to determine pool or riffle preferences. Fish were captured from one electrofishing run, moving upstream using 2 operators, one with a dip net and polaroid glasses. Pools and riffles were separated by stop nets and the wetted perimeter of each section was measured and the area calculated. Fish numbers were adjusted using electrofisher efficiencies provided in Koehn & McKenzie (1985).

All fish sampling was conducted using a Smith Root Model 12 backpack electrofisher operated at settings of 120 Hz and 600 or 700 V. The length to caudal fork (LCF) of each fish was measured to the nearest mm and the spawning condition of each fish was assessed as per maturity stages in Pollard (1972).

Water temperature and conductivity were recorded during each sample using a Yellow Springs Model 33 Conductivity/Temperature meter. Relative water level was measured at a fixed depth gauge on each visit. The habitat at each spawning site was described. In determining pool or riffle preferences (11 July), stream length, width and depth were measured along with observations of the location of each fish collected. Water velocities were measured 100 mm above the substrate using an Ott mini flow meter. Substrate particles were assessed visually, according to the size categories of Cummins (1962).

Fecundities were determined for 7 ripe females collected on 15, 22, 29 August 1990 and for 24 females collected on 11 July 1991 by dissecting gonads, prising eggs apart and counting individually.

Egg searches were carried out in both pools and riffles in the stream by the following methods:

- (1) by inspecting instream habitat such as substrate and wood debris for attached eggs;
- (2) by using drift nets of mouth opening 35×17 cm mesh mm (Hellowell 1986) positioned in the stream for (a) 3 hours and 22 hours where there had been no upstream disturbance of the streambed, and (b) several minutes, 0.5 to 2 m downstream from where substrate or instream cover had been gently disturbed (e.g. by lifting cobbles).

Collected samples were inspected visually for the presence of eggs. Diameters of 50 oocytes and of 28 fertilized eggs collected from the field, and lengths of 16 newly hatched larvae, were

measured to the nearest 0.01 mm using a Nikon Profile model 6C-2 projector at a magnification of 10 \times .

Eggs collected in the field by the above methods were transferred to hatching baskets in the aquaria and the time taken to hatch was recorded. The hatching baskets consisted of 80 mm lengths of 90 mm diameter PVC pipe covered at one end with 0.5 mm nylon mesh netting. These baskets were suspended vertically in a 20 L aquarium tank with a through flow of approximately 27 L/h of filtered, dechlorinated water (aquarium water) (see Bacher & O'Brien 1989). Water temperatures were maintained between 12.3° and 14.9°C.

Sixty larvae hatched from collected eggs were placed in three 4 L tanks (20 per tank) filled with static, aerated aquarium water kept at ambient temperatures of 15.0°C to 17.2°C and the time taken to use up their yolk sacs observed.

The time to first feed was determined by placing 20 5-day-old larvae which had used their yolk sac in a tank to which 250 mL of water from a swamp containing abundant plankton was added. Larvae and water were then removed to a beaker twice daily and any feeding activity observed using a stereomicroscope. Guts were checked for food particles.

RESULTS

Habitat preferences

It was estimated that more than 90% of *G. olidus* collected in 1990 were from pools containing areas where water velocities were 0–0.15 m/sec, depths were 0.4–0.7 m, and there was abundant instream cover in the form of wood debris, submerged tree roots and undercut banks. The substrate of pools varied from predominantly silt/clay to boulder and cobbles. Sampling of 5 pools and 4 riffles on 11 July 1991 showed that 87% of *G. olidus* came from pools. Calculated on a per area basis, 85.5% of *G. olidus* occurred in pools and only 14.5% in riffles.

Two sections of the stream 22 m and 95 m long were electrofished on 4 October and 25 October 1990. Population densities of 1.09 and 0.84 fish/m² respectively were removed from one electrofishing run. Koehn & McKenzie (1985) recorded a 64% capture efficiency for common galaxias, *Galaxias maculatus*, from one electrofishing run using a Smith Root MKVIA electrofisher. These trials were conducted on a similar species, of similar size, under comparable conditions, with equipment considered to be of similar effi-

ciency. The population densities for *G. olidus* were thus adjusted by a factor of 1.56 to give calculated population densities of 1.70 and 1.31 fish/m² respectively.

Population structure

In the length-frequency histogram for the *G. olidus* population (Fig. 2), four size classes were recognised (Table 1). Following Fletcher (1979) these size classes were assigned estimated age classes of O+, 1+, 2+ and 3+ years, with O+ being assigned to juveniles from the 1989 spawning. In the 263 fish captured, the size ranged from 36 mm to 100 mm LCF, the largest fish being ripe females.

Further analysis of the age classes (Table 1) shows that the population was dominated by the 1+ age class, although the smaller O+ age class was likely to be under-represented due to less efficient sampling of smaller fish (Koehn & McKenzie 1985). Only 2.3% of the population were 3 years or older, indicating that few fish live beyond their third year.

Details of sexual maturity for each age-class are given in Table 1. Most *G. olidus* do not reach sexual maturity in their first year (0+) when only 20% of male and 5% of female fish were

sexually mature. The smallest sexually mature male was 42 mm (LCF) and the smallest female was 47 mm LCF. All fish were sexually mature by their second year (1+).

The overall sex ratio of mature fish in the population was 1 : 1 but the ratio of sexually mature individuals was not consistent throughout the age-classes. The earlier maturity of some O+ male fish increased the apparent male : female ratio in that class. The 1+ class showed a 1.1 : 1 ratio whereas the 2+ class showed a 1 : 4.0 ratio. All six fish in the 3+ class were female.

The 31 ripe female *G. olidus* analysed for fecundity ranged between 55 mm and 88 mm LCF (mean 66 mm) and contained from 44 to 384 eggs (mean 198, N = 31, SE = 15). Number of eggs of *G. olidus* is positively correlated to fish length ($r = 0.836$, $p < 0.01$) (Fig. 3).

Spawning season

The spawning season for *G. olidus* in Bruces Creek in 1990 extended from early August to about late October. The percentage of spent fish in each sample increased from 10% to 93% during the study (Fig. 4). Although spawning had already begun by the start of the study, this sam-

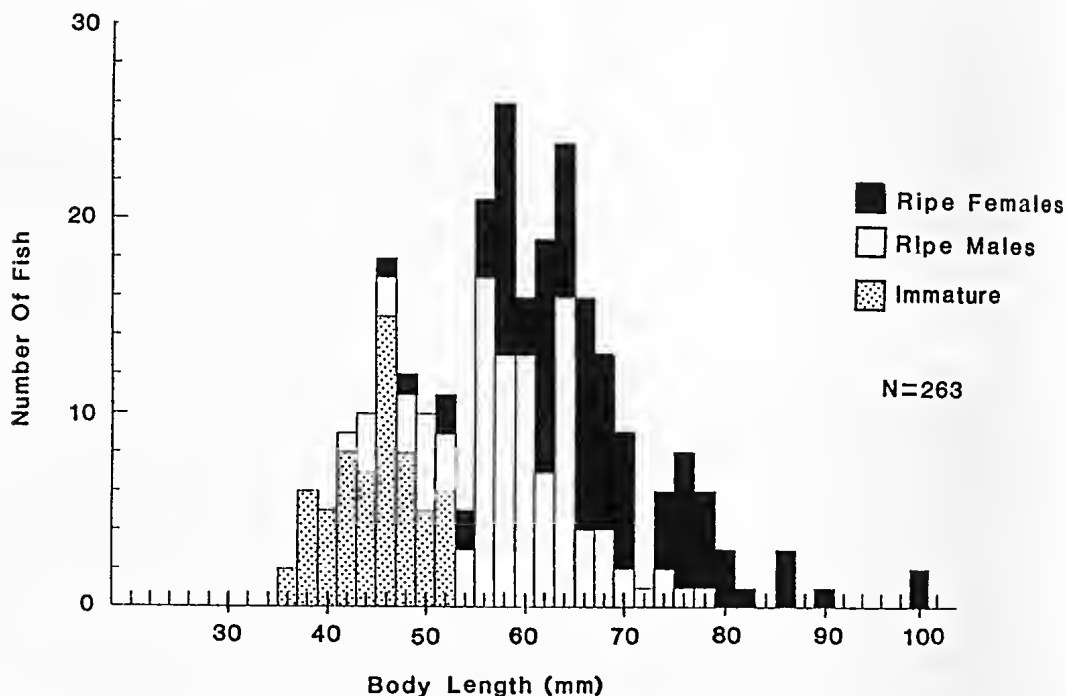


Fig. 2. Length-frequency histogram for *Galaxias olidus* in Bruces Creek in 1990.

Age Class	Length Range (mm)	Fish Nos	% Popn	Ripe Males		Ripe Females		Immature Fish		Male: female ratio
				No.	%	No.	%	No.	%	
0+	36-52	83	31.6	17	20.5	4	4.8	62	74.7	4.1:1
1+	53-72	150	57.0	8.0	53.3	70	46.7	0	0	1.1:1
2+	73-82	24	9.1	4	16.7	20	83.3	0	0	1:4.0
3+	83-100	6	2.3	0	0	6	100	0	0	N/A
Total		263		101		100		62		1.0:1

Table 1. Length range, number of fish collected, percentages of ripe males, females and immature fish, and sex ratios for each age class of the *Galaxias olidus* population during the 1990 spawning season in Bruce Creek.

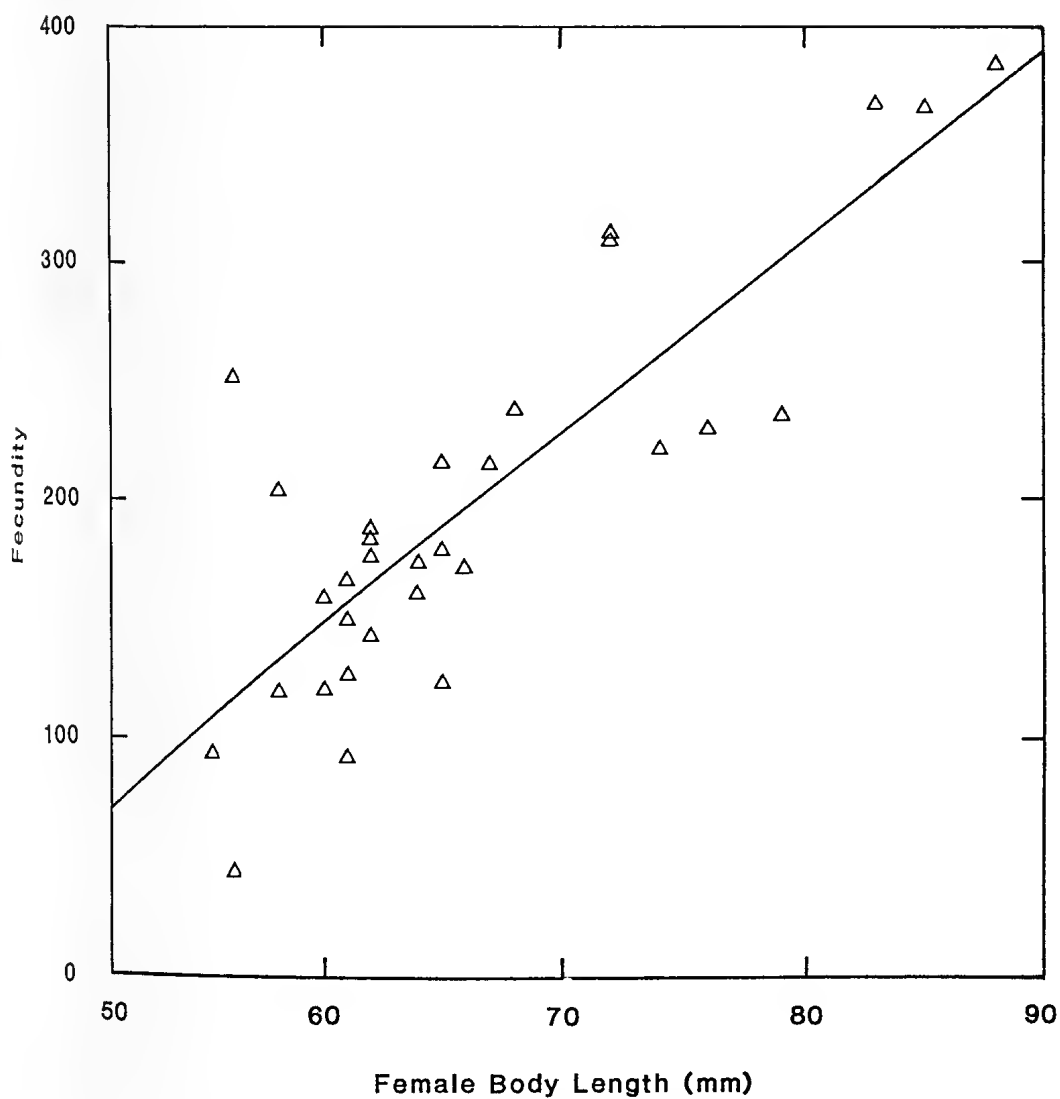


Fig. 3. Relationship between length and fecundity for *Galaxias olidus* females in Bruce Creek.

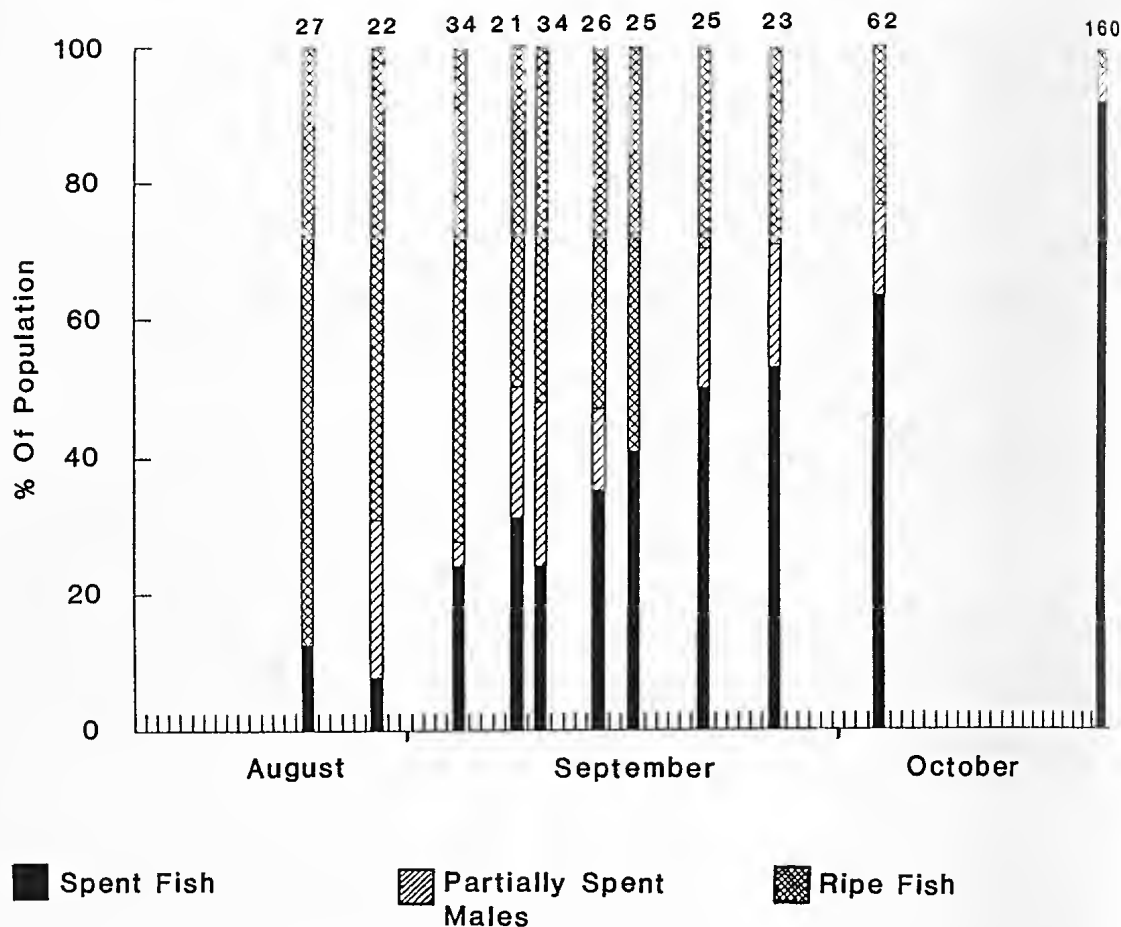


Fig. 4. Percentage of ripe and spent *Galaxias olidus* during the 1990 spawning season in Bruces Creek. Numbers of fish examined are given above each column.

pling period covered most of the spawning season.

Most females collected were either ripe or spent, only two being part spent, an indication that females lay all their eggs at once. Both part spent females had red bruising on their sides and abdomen suggesting they may have been in the act of spawning when captured. Several other females (spent and running ripe) and males (part spent) had similar marks.

Eggs in some gravid females in the 4 October sample and in all gravid females in the 25 October 1990 sample were noticed to be smaller in size, possibly indicating that a small percentage of females did not spawn and were undergoing involution. Throughout the breeding season a proportion of males were partially spent, suggesting that each male may be involved in more than one fertilization.

Daytime water temperatures between 15 August 1990 and 4 October 1990 were between 8.0° and 10.2°C and water levels rose to a maximum recorded level of 70 mm above the normal watermark, although observations indicated that higher short-term levels did occur. Water temperature was 13.5°C on 25 October 1990. Water conductivities varied from 73 to 90 EC units.

Spawning sites

Four individual spawning sites were found: three were at the downstream end of a riffle at the head of a pool containing large numbers of ripe fish, and one was at the head of a riffle immediately downstream of a pool. No fish were collected from the near vicinity of any of the spawning sites.

Eggs were found adhering strongly to the underside of boulders larger than 180 mm in diameter situated in riffles immediately upstream and downstream of pools. Eggs were not found attached to wood debris or other instream objects.

The underside of each boulder was relatively flat but slightly raised (up to 60 mm) from the streambed so that the eggs were sheltered from the main water current. Water velocities in the riffles around the boulders ranged from approximately 0.2 to 0.5 m/sec. On two boulders which had not been disturbed 179 eggs and 26 eggs were counted. Eggs were attached either singly or in groups of 6 to 62; the eggs were usually one and not more than two layers thick and were coated with sand and gravel particles. The boulder with 179 eggs contained eggs at three different stages of embryological development.

In four drift nets set for 3 hours below undisturbed sites only one egg was collected. A repeat set of that net 2 days later at the same site collected one more egg. The net had been positioned in the main gently flowing current (0.1 m/sec) about 1.5 m downstream of a riffle. No eggs were collected in two nets set overnight for 22 hours.

When substrate or instream objects such as wood debris were disturbed by gentle lifting two eggs were caught in one drift net and nine in another held immediately downstream of two riffles. The substrate of these two riffles comprised boulder 10%, cobble 40%, pebble 30% and gravel 20%. One egg was collected from a pool with a "flat" streambed whose substrate comprised sand/silt 70%, boulder 10%, and cobble 10%. No eggs were found in four other pools and three other riffles "searched" in the same manner.

We surmise that most eggs of *G. olidus* are attached to the underside of boulders, but some eggs come to rest in the substrate and a few drift downstream.

Egg description and incubation period

Unfertilised oocytes were spherical, demersal, white or opaque and adhesive. Fertilized, water hardened eggs were spherical, demersal, transparent and initially adhesive but single, unattached eggs became progressively less adhesive.

The diameters of oocytes and fertilized eggs at the earliest stages of development and at the "eyed" stage were:

Mean oocyte diameter = 2.29 mm ($N = 50$, $SE = 0.22$ mm)

Mean egg (early stage) diameter = 2.4 mm ($N = 8$, $SE = 0.11$ mm)

Mean egg (eyed) diameter = 2.29 mm ($N = 20$, $SE = 0.20$ mm).

Three eggs collected on 5 September 1990 were at the earliest stage of embryological development (i.e. no embryo in nucleus) and took 21 days to hatch at temperatures of 12.9–14.8°C. All other viable eggs collected were at later stages of development and hatching times were 9–14 days at 14.0–15.0°C.

Larvae

The lengths of larvae measured 0–6 hours after hatching ranged from 9.0 mm to 9.8 mm TL. Mean length was 9.39 mm ($N = 16$, $SD = 0.26$). The larvae had small yolk sacs 1.4 mm long. In the light, these larvae were active swimmers throughout the water column including at the surface, but they also lay motionless on the bottom of the tank for several minutes. Larvae appeared to have absorbed their yolk sacs after 5 days and commenced feeding 3 days later.

DISCUSSION

Our study provided information on *G. olidus* from relatively natural surroundings unaffected by major habitat alterations or by other fish species including introduced predators. The major habitat preference of *G. olidus* in Bruce's Creek was clearly for pool areas with slow-flowing, deeper water in a stream containing abundant instream habitat of wood debris, submerged tree roots and undercut banks and intact riparian vegetation. Such attributes in streams have been recognised as important for freshwater fishes (Cadwallader & Backhouse 1983, OCE 1988, Lloyd & Walker 1988, Koehn & O'Connor 1990a, 1990b). Riparian vegetation prevents erosion, provides instream habitat and shading, as well as terrestrial invertebrates which form an important element in the diet of *G. olidus* (Cadwallader et al. 1980). McDowall (1980b) has suggested that removal of riparian vegetation correlates with the reduction in population numbers of several galaxias species in New Zealand.

The relatively high population densities of *G. olidus* (1.31–1.70 fish/m²) in Bruce's Creek are comparable to those of 0.79 and 2.83 fish/m² reported by Fletcher (1979) in Watchbox Creek and at Mt Buffalo. Tilzey (1976) reported den-

sities of up to 3.7 fish/m² in tributaries of Lake Eucumbene. Such densities are likely to be attributable to the presence of high-quality habitat and the absence of brown trout, *Salmo trutta*. The effects of *S. trutta* on the abundance and distribution of *G. olidus* have been comprehensively documented, with mutually exclusive populations often occurring and a fragmentation of the range of *G. olidus* resulting in isolated populations often being reported (Tilzey 1976, Cadwallader 1979, Fletcher 1979, Jackson & Davies 1983, Cowden 1988, Jones et al. 1990, Lintermans & Rutzou 1990).

After using otoliths to age *G. olidus*, Cowden (1988) concluded that most individuals did not reach maturity until their third year (age 2+). Drayson (1989), however, examined otoliths from *G. olidus* collected in the same catchment as Cowden and considered their annular patterns to be uneven and therefore unsuitable as a means of accurately aging this species. From the length frequency distribution (Fig. 2), we suggest estimated age classes 0+ (1st year), 1+ (2nd year), 2+ (3rd year) and 3+ (4th year) based on a similar population structure reported by Fletcher (1979). These three age classes make up almost the entire population (97%) of *G. olidus* in Bruces Creek. Most *G. olidus* did not mature in their first year but all were mature by their second year. These results are consistent with those of Fletcher (1979), namely that maturity is mostly reached at age (1+) and that the maximum age is probably 4 years.

Although the sex ratio for sexually mature fish is 1:1, the ratio is not consistent throughout the age classes. Males mature earlier than females but appear to have a higher mortality; consequently females predominate in the 2+ and 3+ age classes. Cowden (1988) also reported a 1:1 sex ratio.

The fecundity of *G. olidus* is one of the lowest among galaxias species in Australia. A mean fecundity of 198 found in this study is similar to the value of 243 recorded by Cowden (1988). Of Victorian galaxiid species, only *Galaxiella pusilla*, a wholly freshwater species, has a similar fecundity (generally 100–200; Humphries 1986). Fecundities of diadromous galaxiid species are generally much higher: common galaxias, *Galaxias maculatus*, up to 13,500 (McDowall 1968); spotted galaxias, *G. trutta-ceus*, up to 16,000 (Humphries 1989); and broad-finned galaxias, *G. brevipinnis*, up to 23,000 (Koehn and O'Connor unpubl. data).

The breeding season of *G. olidus* has been variously reported as winter through to summer

(Cadwallader & Backhouse 1983). *G. olidus* spawns in October in Victorian alpine streams (Fletcher 1979); from early August to early September in the Australian Capital Territory; and during late August to early September in southern Queensland (Marshall 1989). The variation in onset of these spawning seasons may be due to the corresponding differences in water temperatures. Cowden (1988) recorded temperatures of 6.5–8.2°C, whereas Marshall (1989) estimated a temperature range of about 15–20°C. In Bruces Creek the main breeding season extended for over 2 months from early August to about mid October, when the temperature range was 8.0–10.2°C.

G. olidus employed a spawning strategy indicative of a fish species that has a low fecundity and needs to maximise the survival of eggs and larvae. This strategy involves laying a small number (average fecundity of 198) of relatively large (2.3 mm) adhesive eggs in a protected site, usually a boulder more than 180 mm in diameter and with a narrow gap between the underside of the boulder and the streambed. Similar spawning sites for *G. olidus* have been reported by Cowden (1988). In Bruces Creek the eggs were attached to the underside of the boulders where they may be protected from possible predators (especially fish), disturbance, strong water currents and possible smothering by sediment. All the boulders were in riffles where the surrounding water was relatively fast-flowing (0.2–0.5 m/sec) and well oxygenated. Eggs were not found attached to any other instream objects such as wood debris.

Red bruising on the abdomen and sides of many spawning fish of both sexes suggests that the fish rubbed against hard objects during spawning. Bruising is highly likely in enclosed locations where the fish would probably have to press hard against the underside of boulders in a lateral or upside down position to deposit eggs and milt.

A least three different stages of embryonic development were recorded for eggs at one spawning site. Because females appear to lay all their eggs at once, it appears that more than one spawning may take place at a suitable site. The strategy of laying a small number of relatively large, adhesive eggs at an enclosed site has been described for another Victorian freshwater fish, the freshwater blackfish, *Gadopsis marmoratus* (Jackson 1978). *G. marmoratus* attaches its eggs to the inside of hollow logs which are then guarded by an aggressive male fish (Koehn unpubl. data). Parental care of eggs appears un-

likely for *G. olidus* as relatively few fish were collected from the riffle areas and there was no evidence of eggs being guarded. We surmise that ripe males and females from the pools move into the riffles to spawn, then return to their preferred habitat. The collection of eggs in drift nets from both disturbed and undisturbed sites indicates that not all eggs are attached to the spawning site. Such "free" eggs may originate in three ways.

1. Eggs not becoming successfully attached to the spawning site during spawning. This may be expected when fish are attempting to attach and fertilise eggs on the underside of a boulder. There appears to be a large discrepancy between female fecundities and the number of eggs found attached to boulders, suggesting that not all eggs become attached.
2. Eggs being laid at less sheltered sites in the stream where attachment does not occur or where the eggs may easily be displaced. There is, however, no evidence for such sites.
3. Eggs being dislodged from the spawning boulder. This appears unlikely as the eggs adhere strongly to the rock and to each other. Some dislodgement may be possible, however, if subsequent spawning activity occurs at the same site.

The collection of single, non-adhesive, developing eggs at undisturbed sites suggests that some eggs may be carried downstream either by drifting in the current or by rolling along the streambed. Such a mechanism would aid downstream dispersal. *G. olidus* eggs are initially very adhesive, but those at a later stage of development that were unattached were non-adhesive. Some of these eggs probably lodge in the interstices of the substrate in riffles or settle to the streambed in pools. Such eggs were collected by disturbing the substrate.

Hence, the eggs of *G. olidus* may be found in three situations: (a) attached, (b) lodged in the substrate, or (c) drifting. Each of these situations involves a different degree of disturbance to the egg itself, possibly leading to variations in hatching times. Cowden (1988) found that hatching of eggs could be induced by gently swirling the water in which they were held. The induced hatching of eggs of *G. truttaceus* and *G. brevipinnis* by disturbance has also been noticed (Koehn & O'Connor unpubl. data). Cowden (1988) recorded, however, that "induced" fry were smaller and less active than normal.

Exact hatching times were not obtained, but fertilized eggs collected in the stream at an early

embryonic stage took 21 days to hatch at temperatures of 12.9° to 14.8°C. Using Cowden's (1988) results, hatching times were estimated to be 47 days at about 9°C and 32 days at about 13°C. Average temperatures in Bruces Creek from August to mid October were about 9°C, while temperatures in late October were about 13°C. Assuming hatching is temperature dependent, these figures suggest that hatchings in Bruces Creek probably occurred from early October until mid December.

Newly hatched larvae emerged at 9.4 mm TL with relatively small yolk sacs which were fully absorbed after about 5 days, with feeding commencing after a further 3 days. Large, well developed larvae with small yolk sacs are more mobile, able to seek shelter and hence less vulnerable than smaller fry with large yolk sacs. This is consistent with the spawning strategy we have described for *G. olidus*.

Increased sediment input into streams has been recognised as having adverse effects on Victorian native freshwater fish (Cadwallader & Backhouse 1983, OCE 1988, Mitchell 1990, Koehn & O'Connor 1990a, 1990b). Sedimentation would be likely to fill or cover potential spawning sites, and the availability of sites under boulders appears essential for spawning. If such sites were not available or were heavily silted so that eggs do not adhere, spawning may not occur or may have reduced success. Likewise, the loss of interstitial spaces in the substrate due to sedimentation may cause increased mortalities to unattached eggs which normally become lodged there. Eggs of *Gadopsis marmoratus*, *Galaxias truttaceus* and *G. brevipinnis* have shown high mortalities when covered with light layers of silt (Koehn & O'Connor unpubl. data).

Sedimentation and the well-documented threat of predation by introduced species are likely to be major environmental threats to *G. olidus* in otherwise natural streams.

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TAXONOMY AND DISTRIBUTION OF THE AUSTRALIAN TIGER SNAKES (*NOTECHIS*) AND COPPERHEADS (*AUSTRELAPS*) (SERPENTES, ELAPIDAE)

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RAWLINSON, P. A., 1991:12:31. The taxonomy of the Australian tiger snakes (*Notechis*) and copperheads (*Austrelaps*) (Serpentes, Elapidae). *Proceedings of the Royal Society of Victoria* 103 (2): 125–135. ISSN 0035-9211.

The taxonomic histories of species of the Australian snake genera *Notechis* and *Austrelaps* are reviewed. A lectotype is selected for *Hoplocephalus superbus* Günther, 1858 (type species of *Austrelaps*) and neotypes are proposed for the following species: *Alecto fasciolatus* Jan & Sordelli, 1873; *Alecto labialis* Jan, 1859; *Hoplocephalus fuscus* Steindachner, 1867; *Hoplocephalus ramsayi* Krefft, 1864; and *Naja (Hamadryas) scutata* Peters, 1861 (type species of *Notechis*). *Hoplocephalus bransbyi* Macleay, 1878 is a junior objective synonym of *H. ramsayi*. *Hoplocephalus fuscus* and *Alecto fasciolatus* are objective synonyms of each other and junior subjective synonyms of *Hoplocephalus ater*. *Austrelaps labialis* and *Austrelaps ramsayi* are formally removed from the synonymy of *Austrelaps superbus* and given full specific status.

THE SYSTEMATICS of Australian reptiles were poorly understood until recent times. A number of historical problems had contributed to this situation, often including many of the following: (1) type specimens lost or not allocated; (2) type specimens inaccurately or inadequately described; (3) type localities not given, too general or inaccurate; (4) early synonyms overlooked or more recent synonyms not quoted; (5) insufficient attention given to the variability of a species over its whole range; (6) lack of accurate data on morphology and biology, many authors simply repeating earlier accounts; and (7) generic changes of species without re-examination of type specimens.

The publication by Cogger et al. (1983) of a comprehensive catalogue of the Australian herpetofauna rectified many taxonomic errors and clarified the status of most taxa, but several nomenclatural problems remained unresolved. The present paper deals with two such problem taxa, the Australian tiger snakes (*Notechis* spp.) and copperheads (*Austrelaps* spp.).

Abbreviated prefixes of specimen numbers cited herein refer to the following institutions: Australian Museum, Sydney (AM); Natural History Museum, London (BMNH); Museum of Victoria, Melbourne (NMV); South Australian Museum, Adelaide (SAM); Zoologisches Museum, Museum für Naturkunde der Humboldt Universität zu Berlin (ZMB); Zoologisches Museum, Universität Hamburg (ZMH)

SYSTEMATICS

Austrelaps Worrell, 1963a

Type species. Hoplocephalus superbus Günther, 1858.

Remarks. *Austrelaps* was established for the two species *Hoplocephalus superbus* and *Alecto signata* Jan, 1859, but the latter is now assigned to *Hemiaspis* Fitzinger, 1860 (Cogger et al. 1983). The species *superbus* (first as *Denisonia superba* and later as *Austrelaps superbus*) has been recognised by all authors since Boulenger (1896), but Rawlinson (1969, 1971) stated that forms assigned to the species include two distinct morphological groups differing in distribution and ecology. These groups were referred to as the lowlands and highlands forms. A third group from the Mount Lofty Ranges and Kangaroo Island, South Australia, originally regarded by Rawlinson (1969) as an isolate of the highlands form, was recognised by Sutherland (1983) as the Adelaide Hills or pigmy copperhead. This group is referred to herein as the dwarf form. Shine (1987a) stated that the lowlands, highlands and dwarf forms correspond respectively to *A. superbus*, *A. ramsayi* (Krefft, 1864) and *A. labialis* (Jan, 1859). This view has been confirmed in the present study by examination of existing types and reference to original descriptions and illustrations.

Austrelaps superbus and *A. ramsayi* occupy similar habitats in southeastern Australia but *A. ramsayi* is restricted to higher altitudes and more northerly areas (Fig. 1). The distributions of the two species interdigitate and abut in eastern Victoria, particularly in the area south and

west of the Baw Baw Plateau, but the species have not been collected syntopically. *Austrelaps labialis* is known only from two disjunct areas, Kangaroo Island where it is widespread, and the Adelaide Hills roughly within the 1000 mm isohyet.

Key to species of *Austrelaps*

1. Supralabials boldly marked, anteroventral quarter cream, remainder dark brown, the two colours meeting at a sharp diagonal demarcation; lower anterior temporal usually in point contact with or failing to contact lower postocular 2
- Supralabials with weakly defined, narrow whitish anterior margins; lower anterior temporal usually in broad contact with lower postocular; ventrals 143–164 *Austrelaps superbus*
2. Ventrals 150 or more; eastern Victoria to New England region of New South Wales *Austrelaps ramsayi*
- Ventrals 148 or fewer; Kangaroo Island and high rainfall areas in the Mt Lofty Ranges, South Australia *Austrelaps labialis*

Austrelaps superbus (Günther, 1858)

Alecto curta.—Duméril et al. 1854: 1252–1254 (in part; non *Naja curta* Schlegel, 1837).

Hoplocephalus superbus Günther 1858: 181.

Alecto schmidtii Jan & Sordelli 1873: liv. 44, pl 1, fig.

4.
Denisonia superba.—Boulenger 1896: 353 (in part).

Austrelaps superbus.—Worrell 1963: 3 (in part).—Sutherland 1983: 50–52.—Cogger et al. 1983: 218 (in part).

Notechis superbus.—Storr 1982: 235 (in part).

Remarks. Günther (1858) described *Hoplocephalus superbus* on the basis of 15 specimens in the Natural History Museum, London. Six of these were later used by Günther (1863) to erect a new species, *Hoplocephalus minor*, subsequently referred to the new genus *Elapognathus* by Boulenger (1896); one of these six specimens was apparently exchanged to the Zoologisches Museum in Berlin (ZMB 4298) and is presumed lost. The remaining nine syntypes of *H. superbus* have been examined by the author (see Appendix 1) and all are referable to the lowlands form of *superbus*, to which form the species name is here restricted. Several of the syntypes are in poor condition, being soft and with peeling epidermis or damage to the head. The best preserved, BMNH 1946.1.20.37, from "Tasmania" (R. Gunn), is hereby designated the lectotype of *H. superbus*.

Alecto schmidtii Jan & Sordelli (1873, liv. 44, pl. 1, fig. 4) is in colour pattern and proportions a specimen of *Austrelaps superbus* as that species is recognised here. The holotype (ZMH 478),

which has been examined by the author, is in poor condition and bleached, and locality information accompanying it is limited to "1877 Australia".

Austrelaps labialis (Jan, 1859)

Alecto labialis Jan 1859a: 128.

Denisonia superba.—Boulenger 1896: 353 (in part).

Austrelaps superbus.—Cogger et al. 1983: 218 (in part).

Austrelaps labialis.—Shine 1987a: 22.

Remarks. The history of the name *Alecto labialis* has been discussed in part by Coventry & Rawlinson (1980). The species was stated by Jan (1863) to be based on a specimen from New Holland in the Zoologisches Museum at Göttingen, but unsuccessful searches of the collections there by the author and by others suggest that the holotype is lost. No illustration accompanied the initial description (Jan 1859a) but a reprint issued as a separate in the same year (Jan 1859b) included plates with illustrations of the type. Confusion arose when Jan & Sordelli (1873, liv. 44, pl. 1, fig. 1) depicted as *A. labialis* a specimen of a species now known as *Drysdalia coronoides* (Günther, 1858) (see Coventry & Rawlinson 1980).

The illustrations of *A. labialis* given by Jan (1859b) clearly show the boldly diagonally barred labials (described as "half yellow, half black"; see Appendix 2) and the lower anterior temporal well separated from the lower postocu-

lar, both features characteristic of the highlands and dwarf forms of the copperhead but not of the lowlands form. The dwarf form is shorter-bodied than the highlands form, having 135–148 ventrals (mean 141, $n = 30$; one specimen with 157), whereas the highlands form has ventral counts of 150–160 (mean 156.8, $n = 30$). The ventral count of 136 reported by Jan (1859) for *A. labialis* could therefore apply only to the dwarf form. Thus, in the absence of any other available name, the correct name for the dwarf form is *Austrelaps labialis* (Jan, 1859).

In order to stabilise the name, specimen SAM

R26414, a female, from Islet 477, Pelican Lagoon, Kangaroo Island, South Australia, is here designated as neotype. The neotype has the following taxonomically significant features. Midbody scale rows 15. Ventrals 139. Anal single. Subcaudals 43, entire, excepting the last three which are divided. Lower anterior temporal well separated from lower of two postoculars on each side. Supralabials 6/6. Colour very dark brown dorsally, the lateralmost scales grey-white with a dark trailing edge, the size and contrast of the pale area decreasing posteriorly and becoming uniformly dark by midbody. Venter

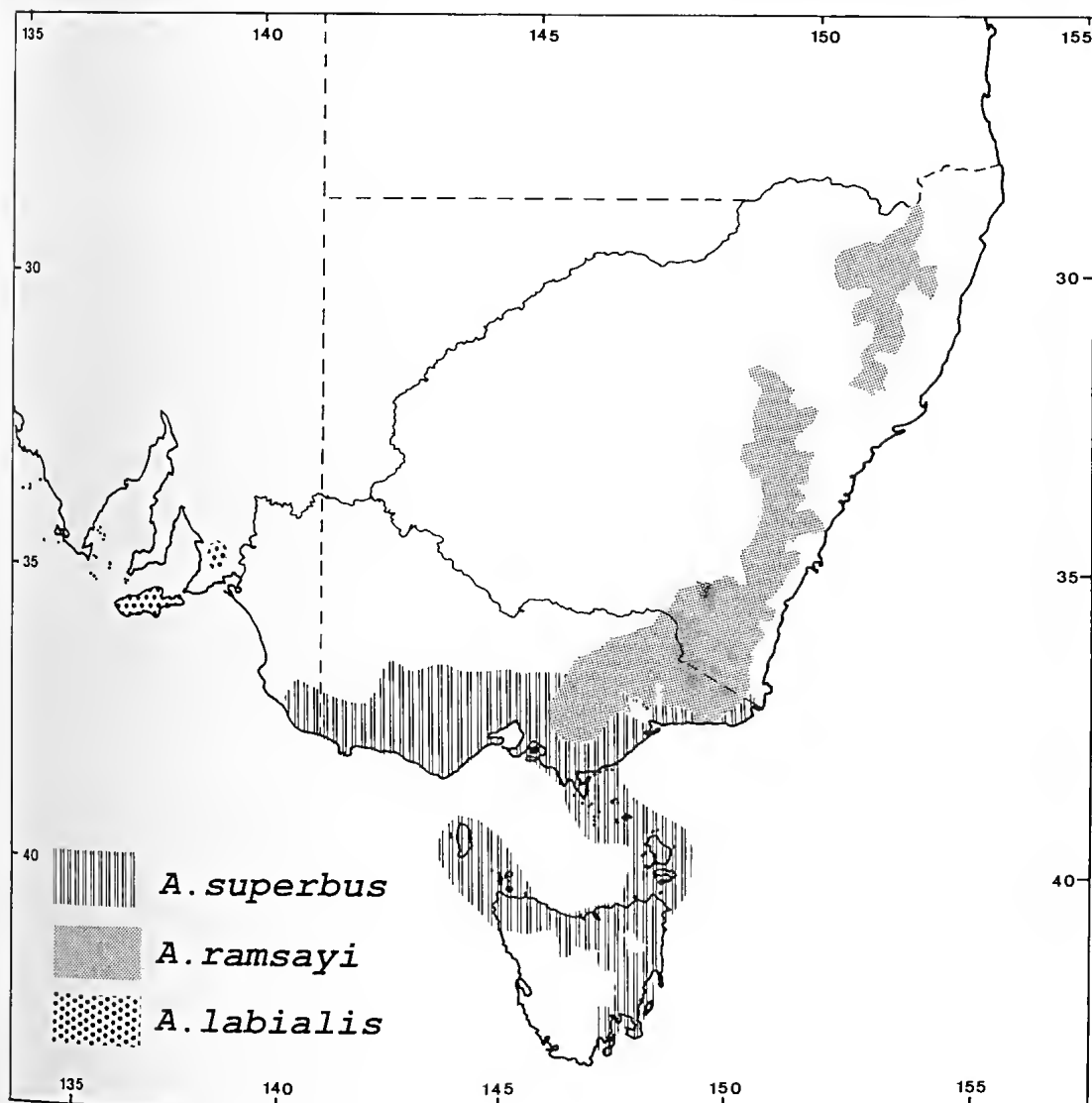


Fig. 1. Distribution of *Austrelaps*.

dark smoky grey, little differentiated from dorsal colour. Chin shields and infralabials cream mottled with medium grey. Rostral, nasals, prefrontals, preocular, lower anterior temporal and supralabial dark brown with a white anterior margin. Most supralabials have the pale colour extending posteroventrally, forming pale triangles. Snout-vent length 450 mm. Tail 104 mm.

***Austrelaps ramsayi* (Krefft, 1864)**

Hoplocephalus ramsayi Krefft 1864: 180.

Hoplocephalus bransbyi Macleay 1878: 52.

Denisonia superba.—Boulenger 1896: 353 (in part).

Austrelaps superbus.—Cogger et al. 1983: 218 (in part).

Austrelaps ramsayi.—Sutherland 1983: 50–52.

Remarks. Searches by the author and others for the holotype of *H. ramsayi*, a small, “apparently young” specimen from the “neighbourhood of Braidwood”, New South Wales (Krefft 1864) have been unsuccessful and the specimen is presumed to be lost. Krefft’s description is of a snake that in scalation and colour, especially the combination of a dark vertebral line, 15 mid-body scale rows and “upper labials and chin-shields whitish, marked with olive-brown in the upper corners”, could only be a juvenile copperhead. The only respect in which the description fails to apply to a copperhead is the divided (“bifid”) anal scale; this is considered to be either an aberration or an erroneous observation. Only one copperhead taxon, the highlands form, occurs in the Braidwood area and thus, in the absence of an earlier available name, the combination *Austrelaps ramsayi* (Krefft, 1864) is the correct name for this taxon.

The holotype of *Hoplocephalus bransbyi* Macleay, 1878 (AM R31922; ex Macleay Museum MR1362, R541), from Moss Vale, New South Wales (34° 33′ S, 150° 23′ E), has been examined and is also a typical highlands form specimen. In order to stabilise the name for the highlands form, the holotype of *H. bransbyi* is here designated as neotype of *H. ramsayi*. Thus, *H. bransbyi* becomes a junior objective synonym of *H. ramsayi*.

The neotype has the following taxonomically significant features: Midbody scale rows 15. Ventrals 151. Anal entire. Subcaudals 46, single. Lower anterior temporal inserted between fifth and sixth supralabials; not in contact with lower of two postoculars. Supralabials 6/6. Colour faded. Light brown dorsally. Narrow dark band

on neck, bordered posteriorly by a light band. Some dark “lines” along neck. Ventral surfaces light brown; anterior half of each ventral and subcaudal scale dark brown. Supralabials and lower anterior temporal dark brown with a sharply demarcated, triangular whitish antero-ventral corner. Snout-vent length 340 mm. Tail 72 mm.

***Notechis* Boulenger, 1896**

Type species. Naja (Hamadryas) scutata Peters, 1861.

Remarks. *Notechis* is closely related to *Austrelaps* and these genera were synonymised by Storr (1982). For several reasons, Storr’s expanded concept of *Notechis* is unsatisfactory (Hutchinson 1990) and traditional usage, with *Notechis* restricted to the *scutatus*-*ater* complex and *Austrelaps* recognised as a distinct genus, is maintained here.

Schwaner (1985a, 1985b), based on work in preparation, believes that all tiger snake populations belong to the single species *Notechis scutatus*. Pending Schwaner’s analysis, and to facilitate discussion, the view adopted here is that two species can be recognised, *N. scutatus* and the black tiger snake, *Notechis ater* (Krefft, 1866). *N. ater* is darker in colour than *N. scutatus* and has scale counts ranging lower. Further comparative work including biochemical analysis over the whole geographic range of *Notechis* is necessary to establish whether sufficient genetic divergence has occurred in the various disjunct populations to warrant the recognition of any of the subspecies listed in this paper. Also, the specific ranking of *N. ater* must be checked as Mitchell (pers. comm.) and Schwaner (pers. comm.) both report intermediacy of tiger snakes from the mouth of the Murray River and from Kangaroo Island, suggesting either local hybridisation or clinal intergradation.

Notechis is restricted to temperate Australia, the distribution shown in Fig. 2 being based on locality data from specimens in the Museum of Victoria and on selected references. In the author’s view, the present disjunct populations of *Notechis* originated from two parent populations. Since the last glacial period, the rise in sea level and the southern climatic shift has fragmented the southern and western population (*N. ater*) and allowed the northeastern population (*N. scutatus*) to migrate southwards and expand into southeastern Australia. Distributions for *N. scutatus* provided by Worrell (1963c) and Cogger (1986: 446) showed the species extending

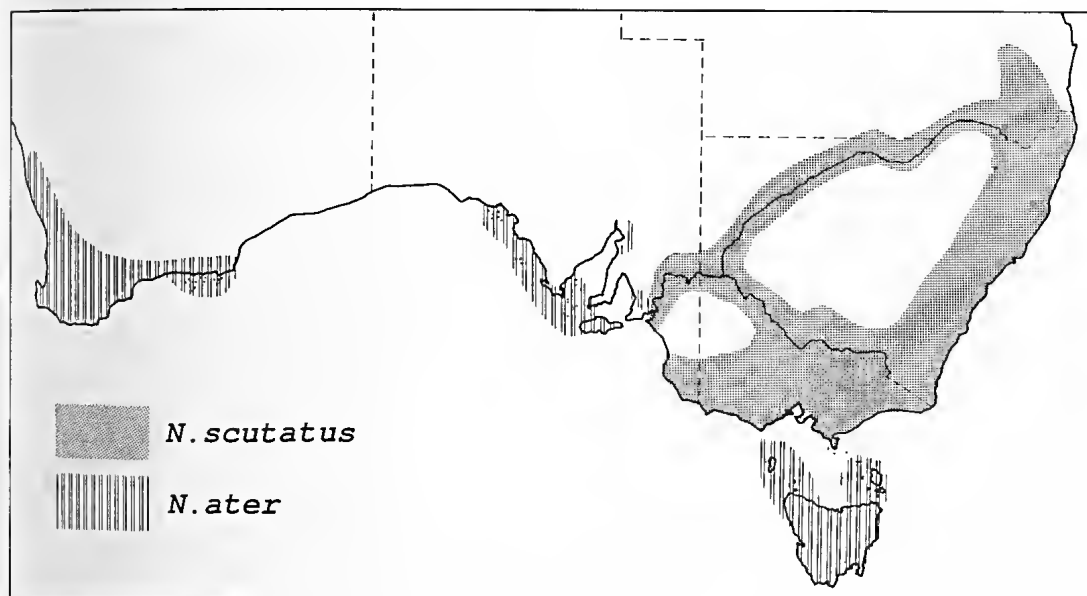


Fig. 2. Distribution of *Notechis*.

farther into the drier interior areas of New South Wales but excluded most of the Darling River and its tributaries.

Notechis scutatus (Peters, 1861)

Alecto curta.—Duméril et al. 1854: 1252–1254 (in part; non *Naja curta* Schlegel, 1837).

Hoplocephalus curtus.—Günther 1858: 216 (in part).

Naja (*Hamadryas*) *scutata* Peters 1861: 690.

Notechis scutatus.—Boulenger 1896: 351 (in part).—Rawlinson 1969: 122.

Notechis scutatus [*scutatus*].—Kingham 1956: 141–142.

Specimens examined. 67.

Scalation. Scales around midbody 17 (11), 19 (55), 21 (1). Ventral scales 158–185. Anal scale entire. Subcaudal scales 36–61, all single. The head and chin shields are similar to those of *N. ater* and there appear to be no consistent differences. As in *N. ater*, the head shields are subject to intraspecific variation. Figures can be found in Waite (1929) and Rawlinson (1965).

Colour. Very variable, green, grey-green or brown dorsal scales traversed by roughly 30 mm wide lighter or darker crossbands. There is also a morph with light brown dorsal scales and no crossbands (Rawlinson 1965, Worrell 1963d). Ventral scales lighter green, grey or brown,

sometimes yellow. Subcaudals the same as the ventrals.

Remarks. Peters (1861) described *Naja* (*Hamadryas*) *scutata* from a single specimen supposedly collected in Java. The holotype, ZMB 2815, cannot be located despite extensive searches by the author and others, and the specimen is presumed lost (Cogger et al. 1983: 229). Peters' description (see Appendix 2) does not apply to any Javanese or even Asian elapid (van Hoesel 1959, Tweddie 1983, Welch 1988), which do not have the lower anterior temporal penetrating deeply between the last two supralabials, and most of which have seven supralabials (six in *Calliophis melanurus*) and at least some subcaudals divided. *Bungarus* Daudin, 1803, the only Asian genus generally lacking divided subcaudals, has only a single anterior temporal (Smith 1943). *Calliophis* Gray, 1835 and *Maticora* Gray, 1835 are also ruled out by their midbody scale count of 15 or fewer. The type locality of Java is therefore in error.

Among the proteroglyphous snakes, Peters' description uniquely fits the Australian elapids in the deeply wedged lower anterior temporal (characteristic of the Australian elapids according to McDowell 1970) combined with entire anal and subcaudal scales. Only the tiger snakes combine these two features, plus 17 midbody scale rows and a transversely banded colour pat-

tern. The tiger snake maxilla has three to six tooth loci following the fang, agreeing with Peters' description of four teeth; the gap separating the last tooth can be interpreted as an empty alveolus rather than a true absence.

As Peters' description of the colour fits the tiger snakes of southern Queensland, New South Wales, Victoria and southeastern South Australia, it seems reasonable, and in view of the species' medical importance, highly desirable, to continue to apply the name *N. scutatus* to the tiger snakes of this area. Accordingly, specimen NMV D47618, a male, is hereby designated as neotype. The specimen was collected at "The Brothers", 10 km NE of Benambra, Victoria (36° 56' S, 147° 45' E) by P. A. Rawlinson, A. J. Coventry and P. B. Mather on 27 January 1976.

The neotype has the following taxonomically important characteristics. Midbody scale rows 19. Ventrals 172. Anal single. Subcaudals 57, entire. Frontal almost as wide as broad. Head uniform olive brown above. Neck and forebody olive brown with indistinct darker brown cross bands, more noticeable laterally than dorsally. Dark bands about 3 scales wide, the lighter interspaces about 2 scales wide. Posterior to this, the dark colour becomes predominant, and the lighter colour is confined to the edges of the scales of the interspaces of the banded pattern. Lower labials, throat and belly bright yellow, darkening to olive yellow posteriorly and to pale olive subcaudally. Snout-vent length 846 mm, tail 172 mm.

Notechis ater (Krefft, 1866)

Hoplocephalus ater Krefft 1866: 373.

Hoplocephalus fuscus Steindachner 1867: 82.

Alecto fasciolata Jan & Sordelli 1873: liv. 43, pl. 6, fig. 4.

Notechis scutatus.—Boulenger 1896: 351 (in part).

Notechis ater.—Kingham 1921: 143.—Rawlinson 1967: 215.—Cogger et al. 1983: 229.

Notechis scutatus niger Kinghorn 1921: 145.

Notechis scutatus ater.—Kellaway & Thomson 1932: 35–48.

Notechis scutatus occidentalis Glauert 1948: 139.—Storr 1982: 235.

Notechis ater ater.—Worrell 1963b: 130.

Notechis ater serventyi Worrell 1963c: 3.

Notechis ater humphreysi Worrell 1963c: 5.

Specimens examined. 74.

Scalation. Scales around midbody 15 (5), 17 (58), 19 (10), 21 (1). Ventral scales 135–184. Anal scale entire. Subcaudal scales 31–59, all single. The head shield is very similar to that of *N. scutatus* but intraspecific variation seems

greater in this species. Supralabials 6 (5). Figures can be found in Kinghorn (1921, 1929, 1956) Kellaway & Thomson (1932), Tubb (1938), Glauert (1957) Worrell (1963c) and Cogger (1986).

Colour. Variable, jet black, slate grey or dark brown dorsal scales, usually with lighter crossbands which are more visible on the anterior half of the body. The bands are narrower than in *N. scutatus* (20 mm or less). Sharland (1962) reported that some Tasmanian specimens are ash grey or light sandy in colour with no trace of bands. The ventral scales are lighter than the dorsal scales. Sharland (1962) and Glauert (1948) recorded that some Tasmanian and Western Australian specimens have yellow anterior ventral scales and crossbands. Schwaner (1984) has commented on reddish-bellied black tiger snakes from Kangaroo Island which had been confused with *Pseudechis porphyriacus* (Shaw, 1794). Subcaudals are usually darker than the ventrals.

Remarks. *Hoplocephalus ater*, described by Krefft (1866) on the basis of a single specimen (AM 6577) from the Flinders Ranges, South Australia, was placed in synonymy with *Notechis scutatus* by Boulenger (1896). Kinghorn (1921) reinstated Krefft's species, placing it in *Notechis* and redescribing the type specimen as the original description was inaccurate. Kinghorn also described a single specimen from Kangaroo Island, South Australia as a new subspecies, *Notechis scutatus niger*, which resembled *N. ater* but was distinguished by the presence of six instead of five supralabials. Kinghorn noted that in coloration and form, the new subspecies most closely resembled Tasmanian tiger snakes. Kellaway & Thomson (1932) identified a series of 49 snakes from Chappell Island in the Furneaux Group, Bass Strait as *N. scutatus niger*, describing and illustrating the variations in head and chin shields and supralabials, and stating that the variation overlapped Kinghorn's descriptions of *N. scutatus niger* and *N. ater*. They therefore reduced *N. ater* to subspecific ranking as *N. scutatus ater*.

Worrell (1963b) reported the discovery of three new specimens of *N. ater* in the Flinders Ranges, stating that, as all had six supralabials, the type was aberrant. He referred to this taxon as *N. ater ater* and listed Kinghorn's *N. scutatus niger* as a subspecies of *ater*. As Kinghorn's separation of *niger* from *ater* on the number of supralabials is invalid, and as Kellaway &

Thomson (1932) showed that variations in a single population overlapped the descriptions of *ater* and *niger*, there seems to be no reason for retaining *niger* as a subspecies and it is here synonymised with *ater*.

Worrell (1963c) described two new subspecies, *N. ater serventyi* from Chappell Island and *N. ater humphreysi* from New Year Island, both in Bass Strait. As these subspecies were based on venom and ecological differences, and as the comparative aspects of the work were not sufficiently comprehensive, there appears to be no reason for the retention of these names.

Glauert (1948) named the southwestern tiger snakes *N. scutatus occidentalis*, basing his description on 40 specimens in the Western Australian Museum, Perth. He compared these with Kinghorn's (1929) scale counts for *N. scutatus scutatus*, assuming these figures to be typical for southeastern Australian specimens. More recent work (Mitchell 1951, Rawlinson 1965), however, has demonstrated that Kinghorn's scale counts were inaccurate, probably being based on Boulenger's (1896) figures for *Brachyaspis curta*. Kinghorn (1956), apparently realising his error, deleted these scale counts from the second edition of his book but provided no alternatives; he also mentioned *N. scutatus occidentalis*, apparently not recognising it. Thus, although Glauert provided a valuable list of scale counts for southern Western Australian tiger snakes, he did not have accurate data on eastern populations for comparison. As Glauert's colour description and scale counts overlap descriptions of eastern populations referred to *N. ater*, this name has been applied to the Western Australian populations by Rawlinson (1974), though Storr et al. (1986) continued to use the combination *N. scutatus occidentalis*.

Two other names, *Hoplocephalus fuscus* Steindachner, 1867 and *Alecto fasciolata* Jan & Sordelli, 1873, have been included by Cogger et al. (1983) in the synonymy of *Notechis scutatus*. Despite searches by the author and others in European collections used by Steindachner and Jan & Sordelli, the type specimens of neither species can be located (Cogger et al. 1983) and are therefore presumed lost.

Most of Steindachner's description of *H. fuscus* (Appendix 2), especially the "vertical" (= frontal) shield that is almost as wide as long and the banded pattern, clearly indicates a tiger snake. All three type specimens, however, were said to have only 15 midbody scale rows, a statistically most unlikely result for mainland tiger snakes. One or both of the larger (unbanded)

specimens could have been copperheads, which have 15 midbody scale rows. However, 15 midbody scale rows are also found in a minority of Tasmanian tiger snakes which are frequently unbanded, and the ventral count given (ca 177) is higher than that recorded in any copperhead population but within the normal range for tiger snakes. It is therefore considered that *Hoplocephalus fuscus* Steindachner, 1867 is a junior subjective synonym of *Hoplocephalus ater*.

The name *Alecto fasciolata* first appeared as a *nomen nudum* in a list in Jan (1863), where the only identifying character noted was a midbody scale count of 17. The illustration in Jan & Sordelli (1873, liv. 43, pl. 6, fig. 4) shows a very well-banded tiger snake in which the pale cross-bands are markedly narrower than the very dark interspaces. Such a combination of colour pattern and scale count is more typical of *N. ater* than of *N. scutatus*. Therefore *Alecto fasciolata* is also regarded as a junior subjective synonym of *Hoplocephalus ater*.

In order to stabilise the status of *Hoplocephalus fuscus* and *Alecto fasciolata*, specimen SAM R14373, a male, from Diprose Lake, Tasmania (41°49'S, 147°22'E), collected by H. Ehmann in February 1973, is here designated neotype of both species. The neotype has the following taxonomically important characteristics. Midbody scale rows 17. Ventrals 173. Anal single. Subcaudals 53, entire (hemipenis reaches to fourteenth subcaudal). Frontal truncate anteriorly, about as wide as long. Head uniform dark brown above. Neck and forebody similar to head in base colour but with indistinct, narrow (about half a scale wide), pale cross-bands becoming more pronounced and broader (to one and a half scales wide) laterally. Dark interspaces about two to three scales wide. Banding disappears dorsally about mid-body and last traces of lateral bands disappear by the last third of the body. Lower labials, throat, and chin olive grey. Anterior ventrals dull yellow with irregular black edgings posteriorly and laterally. Ventral colour darkening to olive grey with less distinct dark edges by mid body, and to dark grey on the posterior belly and subcaudals. Snout-vent length 962 mm, tail 177 mm.

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APPENDIX 1

Notes on the syntypes of *Hoplocephalus superbus*.

BMNH 1946.1.20.37. (Boulenger's specimen e; lectotype herein). Label on jar stating "1946.1.20.37-38, *Denisonia superba* (Types) Tasmania R. Gunn". Snout-vent length (SVL) 594 mm; tail length (T) 131 mm; midbody scale rows (MSR) 15; ventrals (V) 143; subcaudals (SC) 46, all single; anal scale (A) 1; upper labials (UL) 6 (3 and 4 suborbital); lower labials (LL) 7. Frontal 7 mm long by 3.8 mm wide. Rostral 4.5 mm wide by 4.0 mm high. in contact with first upper labial, nasal and internasal scales. Preocular single, in contact with third and fourth upper labials, nasal, prefrontal and supraocular scales. Postoculars 2, in contact with supraocular, parietal, upper anterior temporal, and fourth and fifth upper labials. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.), without [contrasting] dark patches. Specimen in reasonable condition, with some soft patches and peeling epidermis.

The remaining specimens conform to this description except where noted.

BMNH 1946.1.20.40. (Boulenger's specimen a). Label on jar stating "*Denisonia superba* (Type) Australasia 'Ercbus & Terror' Expedition". SVL 848 mm; T 159 mm; MSR 15; V 153; SC 48, all single; A 1; UL 6 (3 and 4 suborbital); LL 7. [Nasal-preocular contact?]. Postoculars 2, in contact with upper[?] anterior temporal. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, being soft and with scales peeling. (Note by AJC and MNH. The author's notes on the type series are very specific in all cases excepting this specimen where they state "Postoculars = 2; supraocular; parietal; temporal; 4 + 5 labial". We interpret this to mean that the lower postocular contacts only the upper anterior temporal. The presence or absence of a nasal-preocular contact is not explicitly stated.)

BMNH 1946.1.20.42. (Boulenger's specimen b). Label on jar stating "*Denisonia superba* (Type) Australasia 'Ercbus & Terror' Expedition". SVL 582 mm; T 123 mm; MSR 15; V 150; SC 45, all single. A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, being soft and with head damage.

BMNH 1946.1.19.6. (Boulenger's specimen c). Label on jar stating "*Denisonia superba* (Type) Australasia

'Erebus & Terror' Expedition". SVL 677 mm; T 133 mm; MSR 15; V 148; SC 45 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, epidermis peeling, and with head damage.

BMNH 1946.1.19.5. (Boulenger's specimen d). Label on jar stating "*Denisonia superba* (Type) Tasmania A. J. Smith". SVL 552 mm; T 108; MSR 15; V 148; SC 41 all single; A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in poor condition, epidermis peeling badly.

BMNH 1946.1.20.38. (Boulenger's specimen f). Label on jar stating "1946.1.20.37-38, *Denisonia superba* (Types) Tasmania R. Gunn". SVL 425 mm; T 99 mm; MSR 15; V 150; SC 46 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.).

BMNH 1946.1.20.34. (Boulenger's specimen h). Label on jar stating "1946.1.20.34-36, *Denisonia superba* (Types) Australia". SVL 644 mm; T 140 mm; MSR 15; V 151; SC 49 all single; A 1; UL 6 (3 and 4 suborbital); LL 6. Postoculars 2, in contact with upper anterior temporal. Temporals 2 + 2. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in reasonable condition, with some soft patches and peeling epidermis.

BMNH 1946.1.20.35. (Boulenger's specimen g). Label on jar stating "1946.1.20.34-36, *Denisonia superba* (Types) Australia". SVL 672 mm; T 140 mm; MSR 15; V 149; SC 47 all single; A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with upper anterior temporal and with fourth and fifth upper labials. Temporals 2 + 3. Upper lip colouration typical of *A. superbus* (s.s.). Specimen in reasonable condition, with some soft patches and peeling epidermis.

BMNH 1946.1.20.36. (Boulenger's specimen i). Label on jar stating "1946.1.20.34-36, *Denisonia superba* (Types) Australia". SVL 154 mm; T 29 mm; MSR 15; V 150; SC 43 all single; A 1; UL 6 (3 and 4 suborbital); LL 7. Postoculars 2, in contact with both anterior temporals. Temporals 2 + 2. Upper lip colouration with dark patches typical of juvenile *A. superbus* (s.s.). Specimen in good condition, with some soft patches.

APPENDIX 2

Original descriptions of species for which original type specimens no longer exist.

Alecto labialis, from Jan 1859b: 21.

"This snake, with a steel-coloured body, is distinguished from its congeners by the labials, half yellow, half black; the lower part of the head [sic, read 'body'] is very dark coloured, except for the head

which is also variegated with yellow and black; tip of tail white; 15 scale rows; after the cloaca, 11. Ventrals, 136; anal single; [sub]-caudals entire, 42; total length, 55"; tail 9". [Translated from French.]

Naja (Hamadryas) scutata, from Peters 1961: 690.

"One anterior preorbital shield much higher than long, 2 postorbitals. Only 6 supralabial shields, the 3rd and 4th abutting the eye; the first lower temporal shield is the same size as a supralabial and extends ventrally between the last two. Scale rows just behind the head 16, at the middle of the body 17. All subcaudals entire. Above olive-coloured, with light, distinct transverse bands on the second half of the body. Underside light greenish yellow, the belly and subcaudal scales with blackish bases. Ventral shields 173, the last (anal) entire, subcaudals 45. Behind the fang the upper jaw bears four solid, grooved teeth, which increase in size from first to last and on each side the first three follow closely after one another, [while] the last (fourth) is separated from them by a larger gap. - Total length 1.30 m; head 0.046 m; tail 0.168 m. - Java." [Translated from German.]

Hoplocephalus ramsayi, from Krefft 1864: 180.

"Scales in 15 rows. Anal bifid. Ventrals 164. Subcaudals 51. Total length 10½"; tail 2". Body rather elongate and rounded; head scarcely distinct from neck, rather high and elongate, with obtuse muzzle; rostral just reaching to the surface of crown; anterior frontals moderate, rounded in front; posterior ones larger, bent down on the sides; one anterior, two posterior oculars, the lower forming about one-fourth of the orbit; vertical narrow, six-sided, much longer than broad; superciliaries nearly the same size as the vertical; occipitals moderate, not forked behind; six upper labials, the third and fourth forming the lower part of the orbit; no loreal, replaced by the elongate nasal, second and third upper labial, anterior ocular and bent down anterior frontal. One nasal, pierced by the nostril; scales moderate, rhomboid, in fifteen rows; tail rather short, scarcely distinct from trunk, tapering; eye moderate, pupil rounded; grooved fang in front, some smaller smooth teeth behind.

Dark olive-green above, each scale tipped with reddish, in particular those on the sides; crown and a narrow vertebral line, one scale wide, somewhat darker than the other parts; this line extends to the root of the tail; upper labials and chin shields whitish, marked with olive-brown in the upper corners. Beneath yellow, each ventral scale with a blackish margin; subcaudals nearly black.

Mr E. P. Ramsay discovered this new Snake in the neighbourhood of Braidwood, N. S. Wales; it is apparently a young specimen, its total length not exceeding 10½ inches."

Hoplocephalus fuscus, from Steindachner 1867: 82.

"Syn. *Hoplocephalus Cuvieri* Fitz. (excl. Syn. et Hopl. Cuvieri Fitz. Syst. Rept. p. 28), Ausb. p. 410.

The specimen from the old collection of the Vienna Museum referred to by Fitzinger in "Systema Reptilium" (1843, p. 28) as *Hoplocephalus Cuvieri* belongs to the *Hopl. curtus* species [of] Schlegel and has nineteen scale rows, while the three specimens bearing only fifteen longitudinal scale rows referred to by the same name by Fitzinger in *Cataloge der österr. Naturf.* (p. 410) perhaps belong to an as yet undescribed species, which, in my opinion, is very closely related to *Hopl. pallidiceps* Günth., if not identical.

Char. The head is elongate and tapers anteriorly, in cross-section it has a quadrangular appearance, the dorsal surface is quite flat, and the mid region of the head not widely bulging; the body is rounded, of thick-set appearance, the tail short with a pronounced taper to a point. The vertical shield is only slightly longer than broad. Of the six supralabials the third and fourth are situated below the eye; the second and third are developed dorsally rather as in *H. pallidiceps*, at times (that is to say among the three specimens on one or both sides of the head) acting as a substitute for the absent loreal shield; in the latter case the undivided nasal shield is abruptly truncated posteriorly, in the former it extends to a narrow point. Temporal shields $2 \div 2$. The upper temporal of the first series is elongate

[and] quadrangular, and contacts both postocular shields anteriorly; the lower, larger temporal shield of the same series is triangular with a dorsally curved broad base and rests with the tapering point of its anterior angle against the lower postocular. The upper temporal shield of the second series sometimes fuses with the scales margining it posteriorly, forming a single very large shield. The body scales diminish rapidly in size moving away from the edge of the belly. The dorsal surface of the head and back is dark brown, towards the edge of the belly the sides of the body are olive green. In the neck region of the smallest specimen of 26 inches [Zoll Länge] the outermost scale row bears a yellow-brown longitudinal band; ventral to this is a wider blackish band, which includes the lateral edge of the anterior ventral shields. In just this one specimen one observes on the back distinct traces of small light yellowish brown crossbands which become markedly broader towards the edge of the belly. The largest specimens of 36–38 inches however are quite uniformly coloured dorsally. The anterior and posterior edges of the ventral scales, or only their anterior edges, have blackish seams. – Subcaudal shields (entire) 48–51; ventral scales circa 177. Origin: New Holland." [Translated from German.]

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